
JOURNAL

OF THE

ARNOLD ARBORETUM

VOLUME 65

OCTOBER 1984

NUMBER 4

SYSTEMATICS OF CENTRAL AMERICAN HELICONIA (HELICONIACEAE) WITH PENDENT INFLORESCENCES¹

W. JOHN KRESS

THE FIRST botanical description of *Heliconia* was by Plumier in his *Nova Plantarum Americanarum Genera* (1703). He provided a short generic description of the genus *Bihai* and polynomials for three taxa: *Bihai amplissimis foliis, florum vasculis coccineis*; *Bihai amplissimis foliis, florum vasculis subnigris*; and *Bihai amplissimis foliis, florum vasculis variegatis*.

In his *Species Plantarum* (1753), Linnaeus included these three taxa in a single species, *Musa bihai*, retaining Plumier's exact diagnoses and placing the "variegatis" variety first. Miller (1754, 1768) and Adanson (1763) considered these plants generically distinct from other species of *Musa* and used the generic name *Bihai*. In *Mantissa Plantarum* (1771), Linnaeus also segregated *M. bihai* into its own genus, *Heliconia* L. He provided a generic description of *Heliconia* and gave a short diagnosis of a species, *H. bihai*, with red cinnabar bracts and yellow flowers. Kuntze (1891; substituting the variant spelling *Bihaia*) and later Griggs (1904, 1915) recognized the earlier generic name and transferred all species of *Heliconia* known to them into *Bihai* Adanson. However, at the International Botanical Congress held in Vienna in 1905, *Heliconia* was reinstated as a *nomen conservandum* (Farr *et al.*, 1979).

Around the turn of the century, a number of workers attempted revisions or summaries of the genus. Petersen (1890) and Kuntze (1891) each listed 25 species. Baker (1893), the first to provide an infrageneric classification of the genus, supplied descriptions and keys for 29 species. In 1900 Schumann summarized the genus for Engler's *Das Pflanzenreich* but added no new species and simply translated abbreviated versions of Baker's earlier descriptions into Latin. Griggs was one of the most knowledgeable students of *Heliconia*, due

¹A part of a thesis (Kress, 1981b) submitted to the Department of Botany, Duke University, in partial fulfillment of the requirements for the Ph.D. degree.

in part to his study of plants in the field. However, he never produced a thorough revision, although he did publish several papers on the genus (1903, 1904, 1915). The last of these papers recognized 48 Neotropical species and contained an infrageneric classification that was more detailed than the one proposed by Baker in 1893.

Since the treatment by Griggs in 1915, there has been no major revision of the genus in its entirety. During the last 65 years, many new species have been described and several regional floristic treatments have added to our knowledge of the variation and diversity within *Heliconia*. Lane began work on the genus at Harvard University in the late 1940's and annotated many herbarium specimens with names of new species and varieties, but unfortunately he never published any of these taxa. Recently, Andersson (1981) has provided a modern revision of the species related to *H. bihai* (sect. *HELICONIA*) that is based primarily on herbarium material and has solved many of the taxonomic and nomenclatural problems of that group. Floristic treatments are available for the heliconias of Guatemala (Standley & Steyermark, 1952), Costa Rica (Standley, 1937), Panama (Woodson & Schery, 1945), Middle America (Smith, 1968), Venezuela (Aristeguieta, 1961), Peru (Macbride, 1936), and the Old World (Green, 1969), but most of the studies are now out of date and incomplete. Recent workers in Costa Rica (Daniels & Stiles, 1979), Nicaragua (Smith, 1977, 1980), Panama (Kress, 1981a), Colombia (Abalo & Morales, 1982, 1983b), Ecuador (Dodson & Gentry, 1978; Abalo & Morales, 1983a), and Brazil (Barreiros, 1971, 1976, 1978; Emygdio, 1975, 1976; Santos, 1978) have described many new species. The work of Daniels and Stiles (1979) in particular is an excellent example of the importance of field work in understanding taxonomic delimitations within *Heliconia*.

INFRAGENERIC CLASSIFICATION

Several infrageneric classifications of *Heliconia* have been proposed (see TABLE 1), each one more complex and composed of more hierarchical ranks than its predecessor. Early authors based their groups solely on the shape of the cincinnal bracts. Later workers also used plant size, leaf orientation, and inflorescence habit and structure to devise more detailed—and supposedly more natural—classifications.

Kuntze (1891) published the first infrageneric taxon above the rank of species. The two species contained within sect. *Taeniostrobis* Kuntze—*Heliconia imbricata* and *H. mariae*—are characterized by imbricate cincinnal bracts. Baker (1893, p. 190) divided the genus into two subgenera, *Platychlamys* Baker and *Stenochlamys* Baker, the former containing all species with “ovate-acuminate, deeply boat-shaped” cincinnal bracts; the latter, species characterized by bracts that are “lanceolate-acuminate, shallowly boat-shaped.” Schumann (1900) followed Baker's classification except that he placed *Platychlamys* in synonymy under *Taeniostrobis* and altered the ranks of these taxa from subgenera to sections.

Griggs's superior knowledge of the genus was reflected in his more complete and less artificial classification. He recognized (1903, p. 644) that infrageneric

TABLE 1. History of the infrageneric classification of *Heliconia*.

BAKER (1893)	SCHUMANN (1900)	GRIGGS (1903)	GRIGGS (1915)*
Subg. <i>Platyklamys</i> Baker	Sect. <i>Taenistrobus</i> Kuntze	Subg. <i>Taenistrobus</i> Kuntze	Subg. <i>Taenistrobus</i> Kuntze
			<i>Episcopales</i> Griggs
			<i>Imbricatae</i> Griggs
			<i>Champneianae</i> Griggs
			<i>Pendulae</i> Griggs
		Subg. <i>Stenochlamys</i> Baker	Subg. <i>Stenochlamys</i> Baker
			<i>Distantes</i> Griggs
			<i>Cannoideae</i> Griggs

*Under the generic name *Bihai*.

groups based upon a single character, cincinnal bract shape, inadequately expressed species relationships: “It is not to be denied that the shape of the branch-bracts [cincinnal bracts] is in a general way correlated with the relationships of the species, but it is only an accidental parallelism without much physiological importance, for there are many exceptions—species quite similar in all respects except that the branch-bracts are sufficiently different to place them in different subgenera. . . .” In a diagnostic key he included three subgenera, *Stenochlamys*, *Platyklamys*, and *Taenistrobus*, defined by plant habit and cincinnal-bract orientation.

Griggs later (1915) replaced this classification with one consisting of two subgenera (*Taenistrobus* and *Stenochlamys*) and six subordinate taxa of unspecified rank. All species known at that time were included in his treatment. Plant habit and height, inflorescence orientation, and distance between adjacent cincinnal bracts were characters used to recognize subgeneric groups. However, the actual phylogenetic relationships within *Heliconia* are much more complex than is represented in Griggs’s final classification.

Some question exists as to whether Griggs formally proposed the six subordinate taxa in his 1915 publication because he did not specify their rank. The International Code of Botanical Nomenclature (Stafleu, 1978) specifies that a new name published before 1953 does not require clear indication of rank. In addition, although no formal descriptions or diagnoses were provided, the taxa were sufficiently differentiated in the key provided by Griggs in the same publication. The names for the infrageneric taxa comply with all the other requirements of the Code for valid publication at that time. Griggs’s infrageneric names must therefore be recognized as validly published but without indicated rank.

In the present treatment, I do not propose any new classification of *Heliconia*. Rather, I have purposefully chosen to study in depth a group of species—those with pendent inflorescences—that has previously been classified as a natural assemblage. Where possible, these species are compared with others not included in this taxonomic group. In addition to broad morphological compar-

isons, I have used information on breeding systems, results from artificial and natural interspecific hybridization, and analyses of pollen structure to assess the phylogenetic status of the assemblage. The information provided here will hopefully establish a foundation upon which a more natural classification of the entire genus can eventually be constructed.

Griggs (1903, 1915) was the first to suggest that species of *Heliconia* with pendent inflorescences are closely interrelated, and he included most of these species in his unranked *Pendulae*. However, by placing several species that he described as having pendent inflorescences (*H. punicea*, *H. mariae*, and *H. curtispatha*) into a group characterized by erect inflorescences (*Imbricatae*), he indicated that inflorescence habit was not necessarily an indication of close relationship.

The present revision includes all Mexican and Central American taxa of *Heliconia* with pendent inflorescences (there are no known species with pendent inflorescences in the Antilles). The nineteen species and eight varieties involved fall into three of Griggs's lower groups, *Imbricatae*, *Pendulae*, and *Distantes*. One object of this study was to test the hypothesis that the pendent inflorescence habit is a uniquely derived state in the genus that characterizes a monophyletic group of species. Ideally, all pendent species, including those from South America, should have been incorporated into the study. Unfortunately, a total revision was not logistically possible due to the large number of species, the wide geographic distribution, and the extensive field work needed to investigate the group adequately. For this reason the conclusions reached here concerning the *Pendulae* can only underestimate the complexity of this infrageneric group. Because of this complexity and our lack of knowledge, it is still premature to assign any rank to Griggs's *Pendulae*. A final statement on the phylogenetic classification of *Heliconia* must await a treatment of the entire genus. An extension of the present revision of the Central American species with pendent inflorescences to include the South American species (approximately 50) is planned.

THE HELICONIACEAE

The proper classification of the order Zingiberales has been debated since 1880, when Bentham and Hooker first established four tribes within the Scitamineae. Subsequent authors have subdivided and altered the rank of each of the original four tribes (see TABLE 2). Most current workers recognize eight families within the order.

Heliconia has always been allied with the *Musa* complex that includes *Orchidantha* N. E. Br., *Musa* L., *Ensete* Horan., *Strelitzia* Banks, *Ravenala* Adanson, and *Phenakospermum* Endl. These genera are recognized as distinct from other members of the Zingiberales by their usually arborescent habit and their flowers with five (or six) pollen-bearing stamens. Lane (1955) presented convincing evidence for segregating *Orchidantha* into a monotypic family, the Lowiaceae (proposed by Hutchinson, 1934). He retained the remaining genera in a single subdivided family, the Musaceae. Subdivision of the family into several ranks, Lane believed, best shows the relationships of the genera. He

TABLE 2. Systems of classification.*

					NAKAI (1941) TOMLINSON (1962) CRONQUIST (1981) DAHLGREN & CLIFFORD (1982) Order: Zingiberales
BENTHAM & HOOKER (1880) Order: Scitamineae	ENGLER & PRANTL (1889) No rank	ENGLER (1900, 1902, 1904, 1912) Order: Scitamineae	ENGLER & PRANTL (1930) Order: Scitamineae	HUTCHINSON (1934, 1959) Order: Scitamineae	
Tribes	Families	Families	Families	Families	Families
Zingibereae	Zingiberaceae	Zingiberaceae Subfamilies Zingiberoideae	Zingiberaceae Subfamilies Zingiberoideae	Zingiberaceae Tribes Zingibereae Hedychieae Globbeae Costeae	Zingiberaceae
		Costoideae	Costoideae		Costaceae
Maranteae	Marantaceae	Marantaceae	Marantaceae	Marantaceae	Marantaceae
Canneae	Cannaceae	Cannaceae	Cannaceae	Cannaceae	Cannaceae
Museae (<i>Musa</i> , <i>Ravenala</i> , <i>Strelitzia</i> , <i>Heliconia</i>)	Musaceae Tribes Museae (<i>Musa</i> , <i>Ravenala</i> , <i>Strelitzia</i>)	Musaceae Subfamilies Musoideae (<i>Musa</i>)	Musaceae Subfamilies Musoideae (<i>Musa</i>)	Musaceae (<i>Musa</i>)	Musaceae (<i>Musa</i> , <i>Ensete</i>)
		Strelitzioideae Tribes Strelitzieae (<i>Strelitzia</i> , <i>Ravenala</i>)	Strelitzioideae Tribes Strelitzieae (<i>Strelitzia</i> , <i>Ravenala</i>)	Strelitziaceae (<i>Strelitzia</i> , <i>Ravenala</i> , <i>Phenakospermum</i> , <i>Heliconia</i>)	Strelitziaceae (<i>Strelitzia</i> , <i>Ravenala</i> , <i>Phenakospermum</i>)
	Heliconieae (<i>Heliconia</i>)	Heliconieae (<i>Heliconia</i>)	Heliconieae (<i>Heliconia</i>)		Heliconiaceae (<i>Heliconia</i>)
		Lowioideae	Lowioideae	Lowiaceae	Lowiaceae

*After Tomlinson (1962).

argued that *Heliconia* is the most divergent genus, more closely allied to *Musa* than to the other three genera. After extensive anatomical studies of the order, Tomlinson (1962) concluded that all eight divisions of the Zingiberales exhibit about the same degree of morphological and anatomical differentiation, and that each should be regarded as a family. He therefore followed the suggestion of Nakai (1941) and recognized the Heliconiaceae (including only *Heliconia*) and the Strelitziaceae (comprising *Strelitzia*, *Ravenala*, and *Phenakospermum*) as distinct from the Musaceae (containing *Musa* and *Ensete*). Recent studies on pollen of the Zingiberales (Kress *et al.*, 1978; Stone *et al.*, 1979, 1981) support Tomlinson's morphological and anatomical evidence for the recognition of the Heliconiaceae, and his classification is accepted here. Other recent authors (Stebbins, 1974; Takhtajan, 1980; Cronquist, 1981; Dahlgren & Clifford, 1982) have also adopted this classification.

MORPHOLOGY

The distinctive morphology of members of the genus *Heliconia* merits a short descriptive summary. The following descriptions are taken from observations of living plants and in some cases are not readily applicable to dried herbarium specimens. Although not all character states discussed (e.g., shoot habit, leaf venation, pedicel twisting) are applicable to species with pendent inflorescences, they are nonetheless included to facilitate comparison with other species and to aid workers unfamiliar with the genus.

LIFE FORM

The genus comprises medium to large erect herbs often with extensive sympodial rhizomatous growth (Bell & Tomlinson, 1980). The patterns of production of rhizomes, rhizomatous branches, and erect shoots result in varying capacities for vegetative colonization and differ among species. An investigation of interspecific variation in rhizome morphology and branching pattern may yield information of taxonomic value. Each erect shoot is composed of a pseudostem and leaves, and it is often—although not always—terminated by an inflorescence (FIGURE 1). The pseudostem is made up of an axis covered by overlapping sheathing leaf bases, can be up to several meters in length, and has various colors and textures. In some species (e.g., *Heliconia platystachys*) the pseudostem has a distinctive white, waxy bloom.

LEAVES

Leaf arrangement is distichous. If the leaves are oriented vertically and have long petioles, the plants have the aspect of a banana plant and are called “*Musa*-like” (FIGURE 1, A). If the leaves are more or less horizontally positioned and the blades are short petiolate or essentially sessile on the pseudostem, the plants have the aspect of a ginger plant and are called “*Zingiber*-like” (FIGURE 1, C). These terms correspond to the somewhat confusing terms “musoid” and “can-noid,” respectively, of other authors (Schumann, 1900; Griggs, 1915; Smith,

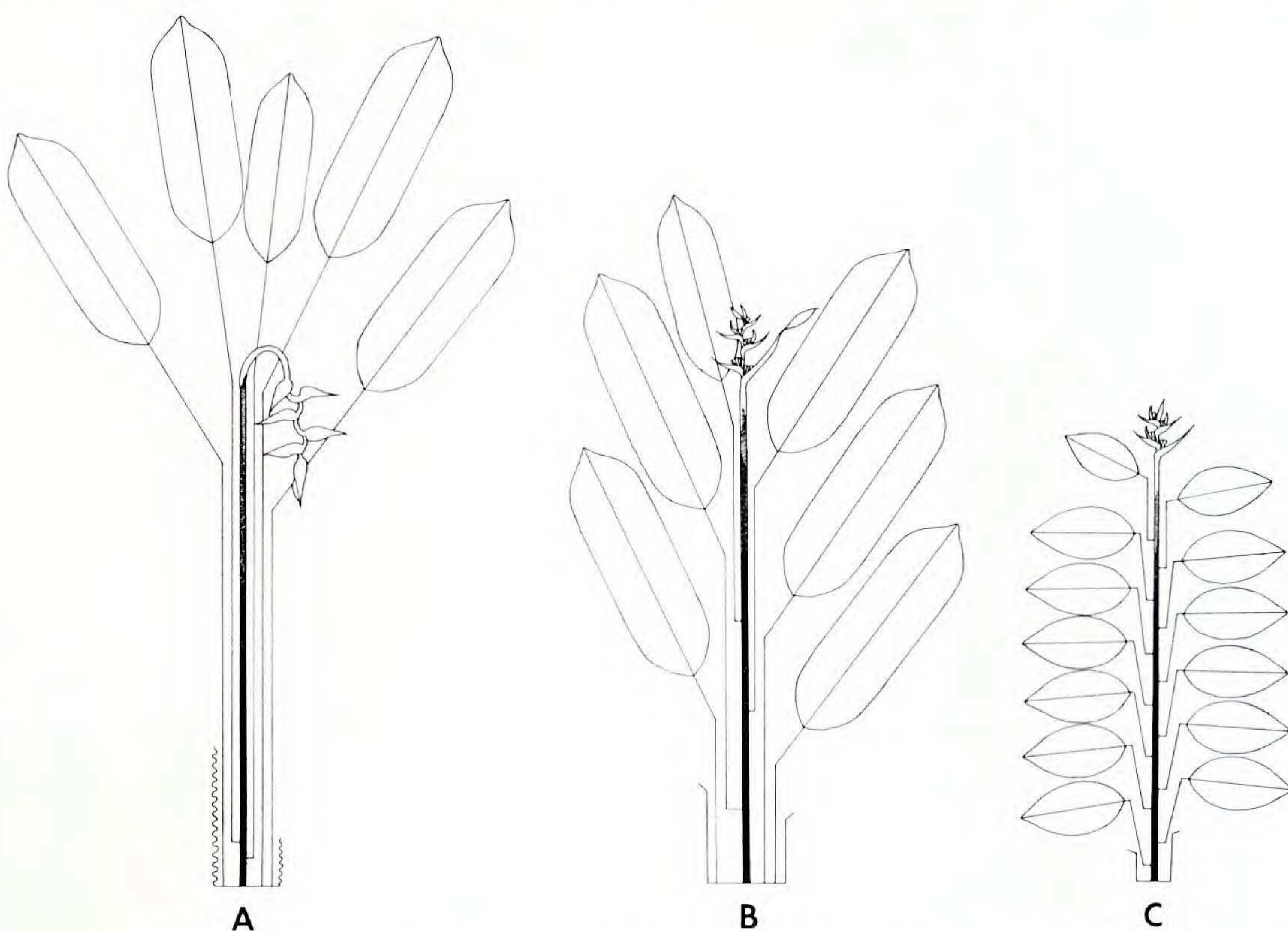


FIGURE 1. Schematic representation of the 3 types of shoot organization in *Heliconia*: A, *Musa*-like; B, *Canna*-like; C, *Zingiber*-like.

1968; Daniels & Stiles, 1979; Andersson, 1981; Abalo & Morales, 1982, 1983a). Some species may have short or medium-length petioles with blades that are held obliquely, and they indeed have a shoot organization resembling that in species of *Canna*. Such plants are called “*Canna*-like” (FIGURE 1, B). The leaves of a single shoot in *Zingiber*-like species usually lie in a single plane. This same planar configuration is characteristic of some *Musa*-like species (e.g., *Heliconia maculata*, *H. trichocarpa*) whose leaves often fan out from stream banks or from the slopes of small embankments.

Lateral veins run perpendicular or oblique to the central midrib (Tomlinson, 1959). Abaxial venation, although usually green and obscure, is sometimes distinctive in color (e.g., in *Heliconia reticulata*), and the midrib usually differs from the lamina in color and texture both adaxially and abaxially.

The lamina is usually green, but in some species (e.g., *Heliconia ramonensis*, *H. secunda* var. *viridiflora*) it is often tinted maroon or red abaxially, especially along the margin. In most species it is elliptic-oblong, coriaceous, entire, and glabrous adaxially and abaxially. Notable exceptions are oblanceolate blades (in the *trichocarpa* group), those that split into narrow lateral segments with age (e.g., in *H. magnifica*), and those having a thick, white, waxy bloom abaxially (e.g., *H. curtispatha*, *H. collinsiana* var. *collinsiana*). The apex is acute to acuminate, and the base is nearly always unequal, with one side extending farther along the petiole. In most cases the base is obtuse to truncate, but it can be cordate, or even attenuate along the petiole (e.g., in *H. maculata*).

INFLORESCENCES

Inflorescences are almost always terminal on erect, leafy shoots, but in a few species (e.g., *Heliconia metallica*) they may arise on a basal leafless shoot. When terminal, the inflorescence may have an erect or pendent orientation with respect to the leafy shoot from which it emerges (FIGURE 1). In some taxa (e.g., *H. secunda*, *H. sessilis*, and some hybrids between erect and pendent species) the inflorescence is carried in an intermediate, nodding posture. The peduncle (the part of the stem between the terminal leaf sheath and the basal cincinnal bract; FIGURE 2, A) may have various colors and textures. The inflorescence is made up of modified leaflike structures called cincinnal bracts ("branch-bracts" or "spathes" of previous authors), the rachis connecting adjacent cincinnal bracts, and a cincinnus of flowers within each bract. Measurements of inflorescence length do not include the peduncle. The rachis (FIGURE 2, B) may differ from the cincinnal bracts in color and texture and is either straight or flexuose (zigzag). Rachis-internode length is measured between two adjacent cincinnal bracts (FIGURE 2, C). The cincinnal bracts are distichous or are spirally arranged due to twisting of the rachis. In some species (e.g., *H. xanthovillosa*) the rachis is only slightly twisted, making the cincinnal bracts subspirally arranged. Each bract is oriented at an angle of from 0 to 180° to the axis of the inflorescence (FIGURE 2, F). The cincinnal bract closest to the peduncle is the basal bract, is often sterile, and may be elongated and leaflike (FIGURE 2, D). The most conspicuous feature of a fertile plant is the colorful inflorescence. The cincinnal bracts are usually bright red and/or yellow but are sometimes green (e.g., *H. talamancana*) or even pink (e.g., *H. colgantea*). In some species (e.g., *H. stilesii*, *H. maculata*) the bracts are glabrous or essentially so, while in others (e.g., *H. magnifica*, *H. xanthovillosa*) the entire inflorescence may be covered by long, woolly hairs. Inflorescence and flower parts may be glabrous, puberulous, tomentose, velutinous, villous, or woolly. The term scurfy is used for any exfoliating vestiture that is easily removed by slight abrasion. The color and texture of the cincinnal bracts generally differ on the inside and outside surfaces. Because the cincinnal bracts decrease in size toward the apex of the inflorescence, those situated in the middle portion of the inflorescence (FIGURE 2, E) are best for comparative measurements. Bract length is measured from the rachis to the distal tip (FIGURE 3, Aa). The width is not measured across the open top since this changes with age, but from margin to margin as if the bract were spread out flat (FIGURE 3, Ab). Mean length/width quotients (l/w) are indicative of general bract shape. Bracts with quotients greater than 2 have long-acuminate apices; those with quotients less than 1.3 have short-acuminate or acute apices. The margins of the cincinnal bracts may be straight, revolute, or involute near the rachis.

FLORAL BRACTS

Each flower of the cincinnus is subtended by an individual floral bract (FIGURE 2, G). Often there are several basal floral bracts that do not directly subtend any individual flower. The floral bracts of some species are opaque and coriaceous, persisting through fruit development to protect maturing ovaries, while

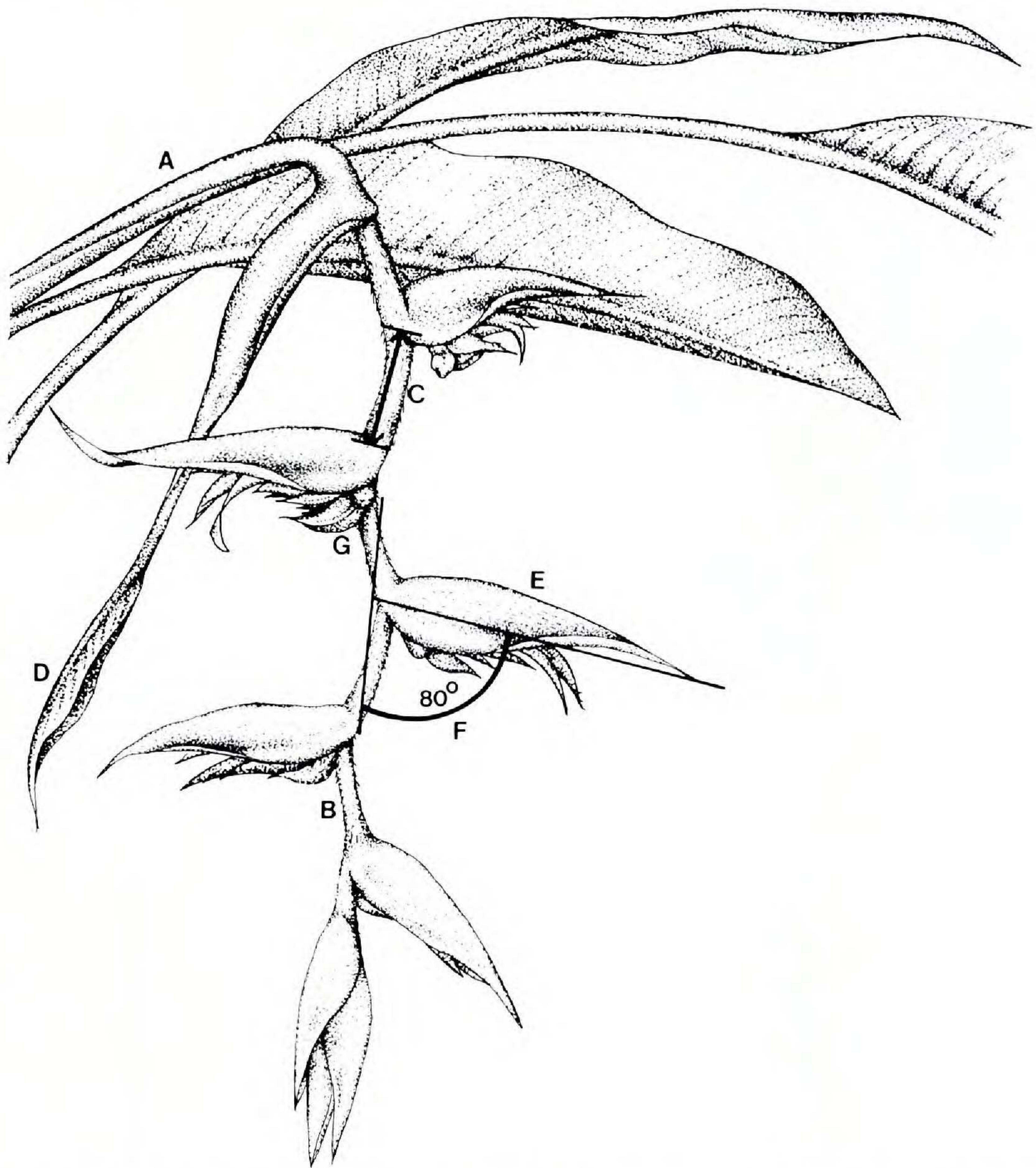


FIGURE 2. Structure and measurements of inflorescences of *Heliconia*: A, peduncle; B, rachis; C, rachis internode length; D, basal cincinnal bract (sterile, with elongated leaflike extension); E, middle cincinnal bract; F, cincinnal bract angle with axis of inflorescence (e.g., 80°); G, floral bract.

those of other species are filmy or translucent and quickly decompose after anthesis. The floral bracts are variously colored and are textured abaxially; the adaxial surface is always glabrous.

FLOWERS

Although most floral characteristics are poorly preserved in pressed and dried plants, they can be quite helpful and even diagnostic when the flowers are fresh (or, in some cases, rehydrated). The flowers are hermaphroditic. Each cincinnus contains several to many (up to 50) flowers. The pedicel (FIGURE 3, Bg) is

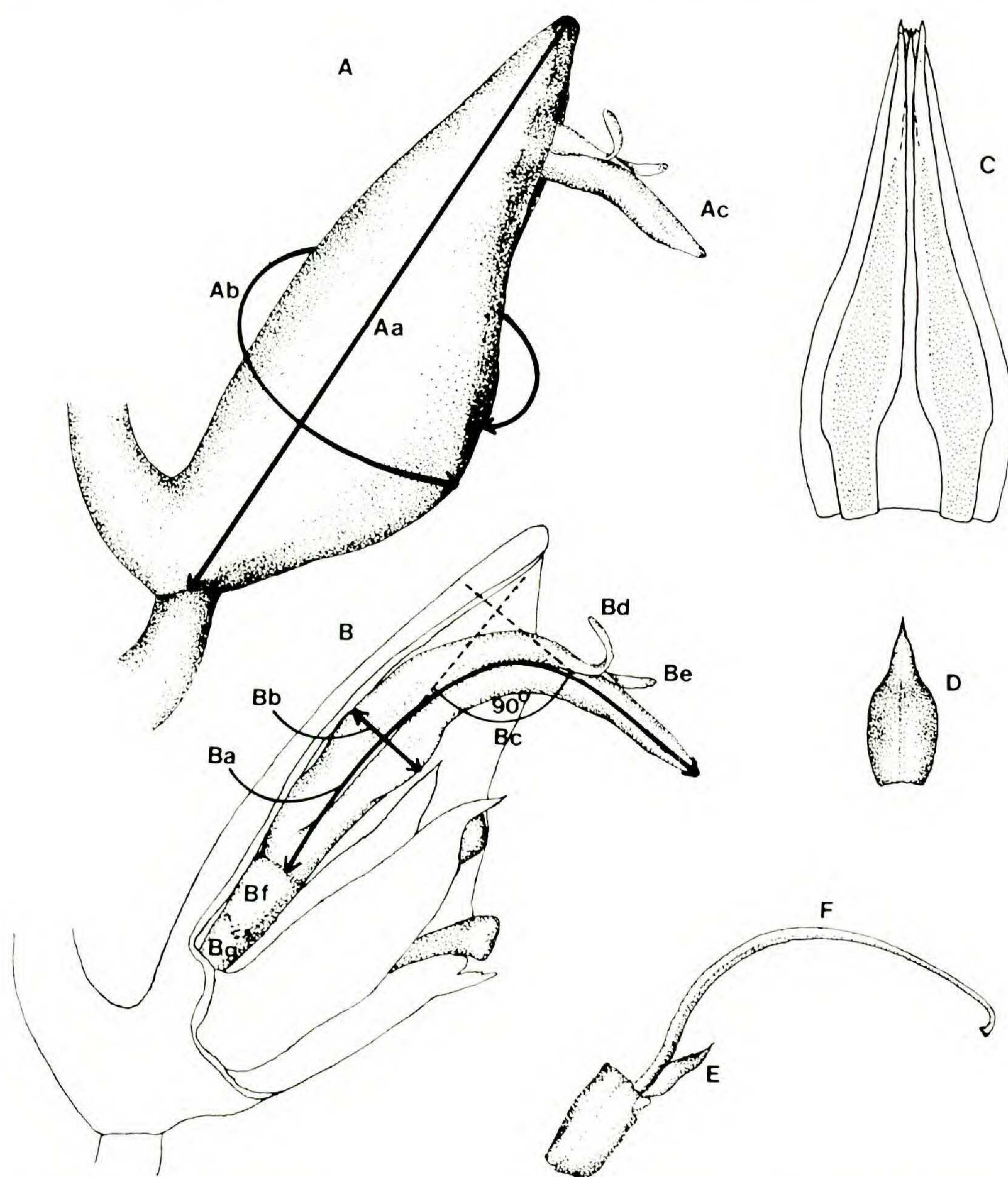


FIGURE 3. Structure and measurements of cincinnal bracts and flowers of *Heliconia*. A, cincinnal bract (Aa, length; Ab, width; Ac, flower protruding at anthesis). B, flower (Ba, perianth length; Bb, perianth width; Bc, perianth angle (e.g., 90°); Bd, apex of fused sepal reflexed; Be, apex of fused sepal not reflexed; Bf, ovary; Bg, pedicel). C, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. D, E, staminodes: D, abaxial view; E, position relative to style, lateral view. F, style and stigma.

usually short and obscured by the floral bracts, but it can be exposed and distinctive in some species (e.g., *Heliconia collinsiana*, *H. trichocarpa*). The perianth is made up of two whorls united at the base that show varying degrees of fusion within and between whorls. At anthesis the single adaxial sepal becomes free from the other perianth members (FIGURE 3, Ac) and allows legitimate pollinators to enter the floral tube. The apices of the abaxial sepals are free from the corolla tube and may be reflexed (FIGURE 3, Bd) or not (FIGURE

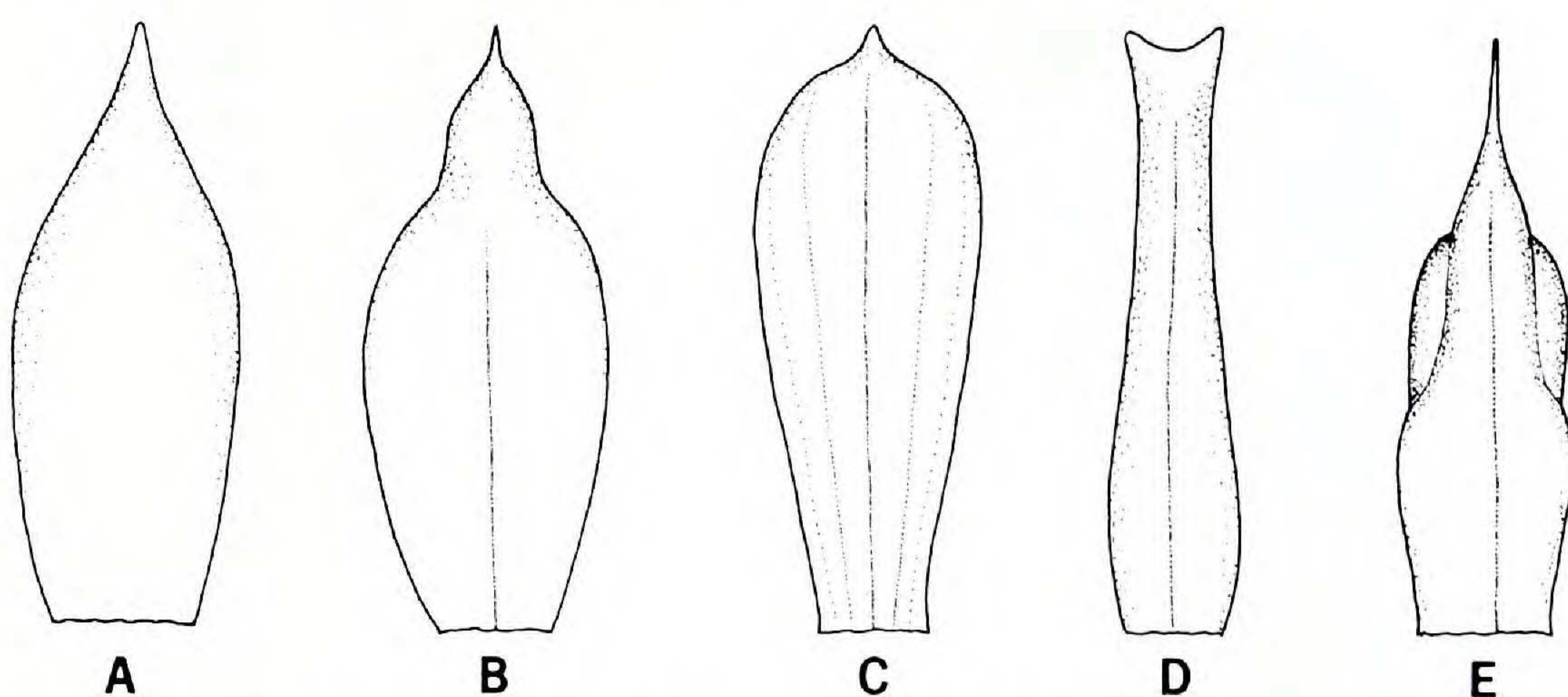


FIGURE 4. Staminode shape in *Heliconia* (not to scale): A, acuminate; B, cuspidate; C, apiculate; D, bidentate; E, lobed.

3, Be). The corolla tube is split along the margins of the two adaxial petals. The partially fused corolla tube is adnate to the two fused abaxial sepals (FIGURE 3, C) and lies opposite the free sepal. The free sepal opens above in erect inflorescences and below in pendent ones. In some species with erect inflorescences (e.g., *H. imbricata*), the pedicel is twisted, causing the flower to be resupinate and therefore to open in a fashion opposite to that described above. The perianth is usually yellow, varying from pale yellow to white at the base and to deep yellow apically. In some taxa the flowers are green (e.g., *H. secunda* var. *viridiflora*) or pinkish red (e.g., *H. mariae*). The sepals can be glabrous or pubescent, and the free sepal is sometimes velutinous or even woolly (e.g., *pogonantha* group). The length and curvature of the perianth tube reflects the length and curvature of the bill of the pollinating hummingbird. The length of the perianth is measured from its articulation with the ovary to the tip of the free adaxial sepal, following any curvature of the tube (FIGURE 3, Ba); the width at its widest diameter (FIGURE 3, Bb). Following the terminology of Andersson (1981), the perianth tube may be slightly curved (e.g., *H. collinsiana*), parabolic (e.g., *H. stilesii*, FIGURE 3, Bc), or sigmoid (e.g., *H. trichocarpa*).

Five stamens are fertile and produce viable pollen. The anthers, borne at the ends of long filaments that traverse the length of the perianth, are either connivent inside the corolla or flared outside of the perianth apex, and they dehisce longitudinally. The sixth stamen is replaced by a staminode located opposite the free sepal (FIGURE 3, D, E). This modified stamen does not produce pollen but may function in some species as a guide leading the hummingbird's tongue to the floral nectaries situated at the base of the style. The staminode ranges in length from 5 to 20 mm, and the apex may be acuminate, cuspidate, apiculate, dentate, or lobed (FIGURE 4).

The ovary (FIGURE 3, Bf) is inferior and three-locular. Each locule contains a single, basally attached ovule. The hypanthium is white, yellow, or green, and although it is usually glabrous, in some species (e.g., *Heliconia trichocarpa*, *H. maculata*) it is puberulous to pubescent. The style is much elongated, runs

the entire length of the perianth, and may be geniculate near the stigma (FIGURE 3, F). The lobed stigma is surrounded by the five fertile anthers at the apex of the perianth. Stigma morphology (degree of lobing and papilla development) appears to vary among species and may prove diagnostic in future studies.

FRUITS

Previous authors have described the fruits as berries, capsules, and "schizocarpic berries." An early study by Humphrey (1896) on seed development in the Zingiberales demonstrated that the mature fruit of *Heliconia* is a drupe with a stony endocarp enclosing each of the true seeds. This interpretation has recently been reconfirmed (B. Kirchoff, pers. comm.) and is accepted here. The outer pericarp is fleshy, and at maturity the surface layer becomes blue (Neotropical species) or red to orange (Paleotropical species). The fruits are very attractive to birds that disperse the seeds (Skutch, 1933; Stiles, 1979). Each drupe contains from one to three pyrenes. Each seed is surrounded by an exceptionally hard, roughened endocarpic envelope. Unlike the seeds of many other members of the order, those of *Heliconia* do not have an aril. The embryo is poorly differentiated at the time of seed maturity (Gatin, 1908), which may account for the delayed germination of *Heliconia* seeds often encountered by horticulturists.

A NOTE TO COLLECTORS

If an entire inflorescence cannot conveniently be collected, several representative sections (including cincinnal bracts from the base and apex) and the peduncle should be pressed. It is helpful if one cincinnal bract is cut open to reveal the flowers and floral bracts. A portion of the leaf showing the base of the blade and a portion showing the apex should also be collected and pressed.

Several vegetative and reproductive characters are of taxonomic importance but are usually not preserved after pressing and drying. Collectors should record the states of these characters from living specimens in the field:

- Pseudostem: Color and vestiture
- Leaf: Configuration
 - Musa*-, *Canna*-, or *Zingiber*-like
 - Orientation
 - spiral or planar
 - Color of lamina (adaxial and abaxial)
 - Color of midrib (adaxial and abaxial)
- Inflorescence: Position
 - terminal or arising from a basal shoot
- Habit
 - erect or pendent
- Color of peduncle
- Color of rachis
- Color of cincinnal bract (inside and outside)
- Arrangement of cincinnal bracts
 - distichous or spirally arranged

- Flower: Orientation
 resupinate or not resupinate
 Color of perianth and ovary
 Curvature of apices of fused sepals
 reflexed or straight
 Orientation of anthers
 flared outside perianth apex or connivent inside apex
 Shape of staminode

POLLEN

The pollen of *Heliconia* and most of its allies in the Zingiberales (excluding Zingiberaceae and Costaceae) is characterized by a sporoderm significantly different in structure from that of most angiosperms. The normally elaborate protective exine is reduced to a few spinules and a thin ($0.08\ \mu\text{m}$) connective layer covering the surface. The intine, contrastingly, is much thickened ($8\ \mu\text{m}$) and structurally complex (Erdtman, 1966; Kress *et al.*, 1978). Radially striate channels perforate the intine of the distal hemisphere, while a more homogeneous but stratified intine characterizes the proximal hemisphere.

Recently, the ultrastructure (Kress *et al.*, 1978), cytochemistry (Kress & Stone, 1982), and ontogeny (Stone *et al.*, 1979) of *Heliconia* pollen have been described in detail. A systematic comparison of pollen of 27 Central American species of *Heliconia* has been published elsewhere (Kress & Stone, 1983). The results of that study that are pertinent to the present taxonomic revision are briefly summarized here.

The pollen of heliconias with pendent inflorescences is $46\text{--}65\ \mu\text{m}$ in polar diameter and $54\text{--}86\ \mu\text{m}$ in equatorial diameter. The distal radius is $24\text{--}56\ \mu\text{m}$; the proximal radius $8\text{--}29\ \mu\text{m}$. The grains may be euoblate, suboblate, or oblate-spheroidal, and isopolar, subisopolar, or heteropolar. In addition to variation in size, the shape and sculpturing of each hemisphere, which are generally different in a single grain, also vary among species. The distal hemisphere is usually convex (but may be subconvex or planar) and sometimes is truncate or shows constrictions parallel to the equatorial plane. The proximal hemisphere may be convex, subconvex, planar, or subconcave. Although the entire wall of the distal hemisphere resembles the germination aperture of more conventional angiosperm pollen, the grains appear inaperturate. However, the pollen tube invariably emerges from a central region at the distal pole. This central region is the functional germination "aperture" and is often structurally distinct. It may protrude from the pole and be elongated, or it may be rather flattened and partially sunken into the distal surface. Sculpturing of the reduced exine ranges from psilate to granulose to verrucose to spinulose or minutely spinulose. In most species the pattern is different on the two hemispheres.

Statistical analysis of both quantitative and qualitative pollen characters support the recognition of four groups among the 19 species with pendent inflorescences studied: the *pogonantha* group, including *Heliconia pogonantha*, *H. magnifica*, *H. ramonensis*, *H. danielsiana*, *H. xanthovillosa*, and *H. mariae*; the *curtispatha* group, comprising *H. curtispatha* and *H. stilesii*; the *trichocarpa*

group, with *H. trichocarpa*, *H. colgantea*, *H. necrobracteata*, *H. maculata*, and *H. talamancana*; and the *nutans* group, containing *H. nutans*, *H. collinsiana*, *H. secunda*, *H. platystachys*, and *H. marginata*. The polar diameter, the degree of grain polarity, the shape of each hemisphere, the shape of the germination aperture, and the sculpturing of the proximal hemisphere are of particular taxonomic value in delimiting these groups, which are also characterized by other morphological traits (see section on phylogeny). The pollen of *H. sessilis*, however, shares some character states with each of the four groups and so is not easily placed in any of them.

Pollen of the *pogonantha* type (FIGURE 5, A) is large ($60\text{--}65 \times 81\text{--}86 \mu\text{m}$), euoblate to oblate-spheroidal, and heteropolar, with a convex-truncate, spinulose distal hemisphere and a planar, psilate proximal hemisphere. The germination aperture is distinct, flattened, and somewhat sunken.

Pollen of the *curtispatha* type (FIGURE 5, B) is medium sized ($53\text{--}57 \times 66\text{--}70 \mu\text{m}$), suboblate, and isopolar, with a convex to subconvex, spinulose distal hemisphere and a convex, minutely spinulose proximal hemisphere. The germination aperture is distinct and usually sunken.

Pollen of the *trichocarpa* type (FIGURE 5, C) is medium sized ($49\text{--}55 \times 67\text{--}79 \mu\text{m}$), euoblate, and isopolar, with a subconvex to planar, verrucose to spinulose distal hemisphere and a convex, granulose to minutely spinulose proximal hemisphere. The germination aperture is indistinct except for an occasional slight depression in the center of the planar distal face.

Pollen of the *nutans* type (FIGURE 5, D) is relatively small ($43\text{--}56 \times 54\text{--}76 \mu\text{m}$), euoblate to oblate-spheroidal, and subisopolar, with a convex, often constricted, spinulose distal hemisphere and a subconvex to planar, psilate to verrucose proximal hemisphere. The germination aperture is distinctly protruding and sometimes quite elongate.

CYTOLOGY

The cytology of *Heliconia* is poorly known. Of the 14 species for which chromosome numbers have been reported (Bisson *et al.*, 1968; Mahanty, 1970), fewer than half have legitimate names and several are not identified to species. In none of the studies was any voucher specimen designated, and it is unlikely that the majority of specimens were identified correctly. In addition, since only one of the species listed (*H. nutans*, if identified correctly) has a pendent inflorescence, the chromosome counts reported are of little help in the present study.

HABITAT AND GEOGRAPHIC DISTRIBUTION

Members of the genus *Heliconia* are distributed primarily throughout the New World tropics from the Tropic of Cancer in Central Mexico to the Tropic of Capricorn in South America. Most species inhabit moist or wet regions, but some are found in seasonally dry areas. Although heliconias attain their most luxuriant vegetative growth in the humid lowland tropics at elevations below 500 meters, the greatest numbers of species (many locally endemic) are found

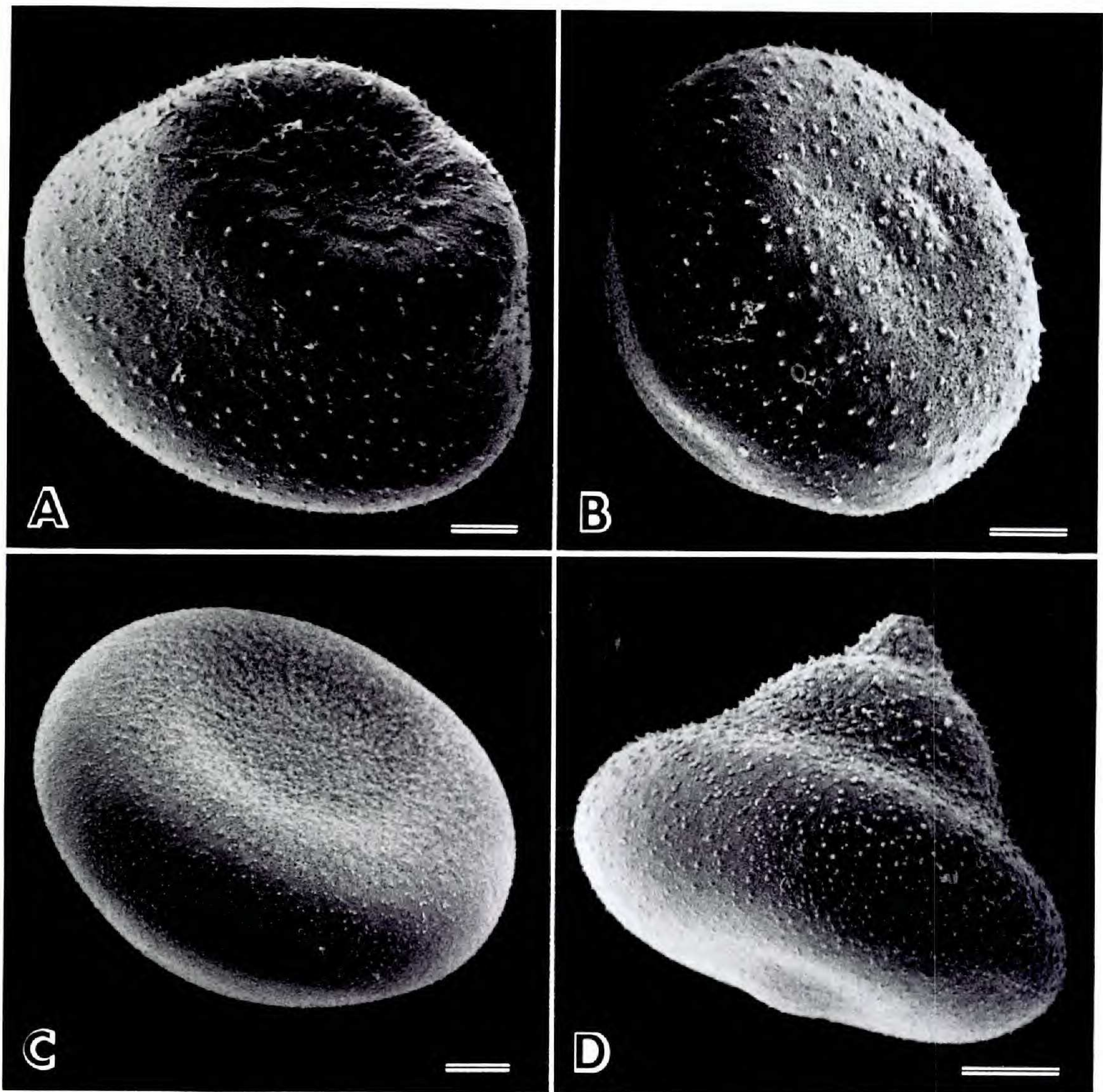


FIGURE 5. Pollen types of *Heliconia* with pendent inflorescences: A, *pogonantha* type (*H. pogonantha*, distal view); B, *curtispatha* type (*H. stilesii*, distal view); C, *trichocarpa* type (*H. trichocarpa*, distal view); D, *nutans* type (*H. nutans*, equatorial view). Scale = 10 μm .

in middle-elevation rain and cloud-forest habitats. Few species occur above 2000 meters.

The most conspicuous members of the genus inhabit open sites in secondary growth along roadsides, on river banks, and in forest light gaps. With increased destruction by man of the tropical rain forest, these species readily invade and colonize the newly opened areas. Other species never attain such extensive vegetative growth and are restricted to the more shaded habitats of the primary forest. These latter species are often locally endemic and are fast becoming extinct as destruction of the forest accelerates.

Species of *Heliconia* with pendent inflorescences are found in Mexico, Central America, South America, and Melanesia (the Solomon Islands). None is known from the West Indies. The taxa treated in this revision are distributed from

Michoacán in southern Mexico to Darién in Panama. Most species occurring north of Costa Rica are found on the wet Atlantic slopes and coastal plains. In Costa Rica and some parts of Panama, the Pacific slopes have sufficient rainfall to support a number of species of *Heliconia*. In these countries several pairs of closely related species (e.g., *H. curtispatha*/*H. stilesii*, *H. trichocarpa*/*H. colgantea*, *H. pogonantha*/*H. danielsiana*) are allopatrically distributed on opposite sides of the central cordillera. No differences in habitat or geographic distribution are apparent between species with pendent and erect inflorescences, and species of the two inflorescence habits are often sympatric.

A curious disjunct group of heliconias is found in the Old World tropics. These heliconias are distributed from Samoa westward to the central Indonesian island of Sulawesi. These plants undoubtedly belong in the genus, even though a separate generic name, *Heliconiopsis*, has been suggested (Miquel, 1859). Green (1969) included all of the Old World taxa in a single species, *Heliconia indica* Lam. A taxonomic treatment currently in preparation (Kress, unpubl.) recognizes eight species occurring in this area, some locally endemic to specific islands or land masses. Two of these species (both unpublished) have pendent inflorescences.

POLLINATION AND REPRODUCTIVE BIOLOGY

Several original reports and review papers describing the reproductive biology of *Heliconia* have recently appeared (Stiles, 1975, 1979; Kress, 1981b, 1983a, 1983b, in press). Only the taxonomically important aspects will be summarized here; see the cited papers for details.

In the Neotropics hummingbirds are the exclusive pollinators of *Heliconia*. Species-specific relationships between birds and plants are rare. Any *Heliconia*, however, can be categorized as being visited primarily either by traplining hermit hummingbirds or by territorial nonhermit hummingbirds (Linhart, 1973; Stiles, 1975). Physiological self-incompatibility is uncommon in the genus; most species that have been tested so far are self-compatible (Kress, 1983a). Plant/bird morphological specialization, hummingbird foraging behavior and habitat, and phenological differences may all serve as isolating mechanisms that prevent pollen exchange between species (Stiles, 1975, 1978; Kress, 1983b, in press). Of all the mechanisms restricting interspecific gene flow in *Heliconia*, physiological regulation of foreign pollen germination and pollen-tube growth at the stigmatic surface and in the style is the most important (Kress, 1983b). I have found that in the species tested, pollen of any one species was inhibited at the stigma, within the stylar tissue, or within the ovary of most other species, and that the site of inhibition depended on the species combination and the direction of the cross. Cross-compatibility was uncommon, and hybrid seed was obtained from very few hybrid combinations. Natural hybridization is also rare (Kress, 1981b, 1983b, in press), especially considering the large number of sympatric taxa in the genus. The few hybrids between species with pendent inflorescences known from the wild are discussed in the section on natural hybridization.

The specificity of the interspecific crossability barriers is significant from a

taxonomic standpoint. In my study (Kress, 1983b) at Las Cruces Tropical Botanical Garden in Costa Rica, nine species with pendent inflorescences were crossed in nearly all reciprocal combinations. Each species was categorized by the ability of the style to accept foreign pollen tubes and the ability of the pollen to grow in foreign styles. Species were then grouped together according to the main type of crossability barrier that characterized the pistil and pollen of each (see TABLE 3). For example, in *Heliconia pogonantha*, *H. danielsiana*, and *H. colgantea* foreign pollen is inhibited at the stigmatic surface, and pollen of these species is inhibited on the stigma of most foreign species. In contrast, although foreign pollen is nearly always inhibited at the stigma in *H. collinsiana* and *H. nutans*, the pollen of these species breaks the stigmatic barrier of most other species, and pollen-tube growth is arrested in the style. In the case of *H. mariae*, *H. stilesii*, and *H. curtispatha*, foreign pollen is stopped at the stigma and/or style, and their own pollen does not penetrate foreign stigmas. *Heliconia trichocarpa* has the least specific pistil- and pollen-inhibition barriers of the nine species tested. When compared to the groups of species recognized by their vegetative, floral, and pollen characters (see section on phylogeny), the groups defined by crossability barriers are nearly the same, even though the placement of some species (e.g., *H. colgantea* and *H. mariae*) is inconsistent. Presence of specific crossability barriers appears to reflect the phylogenetic history of at least some species of *Heliconia*.

PHYLOGENY

One goal of taxonomic investigations is to reconstruct phylogenetic relationships. Phylogenetic systematics (*sensu* Hennig, 1966), or cladistics, provides a logical and repeatable method for formulating hypotheses of phylogeny and for devising biological classifications (Bremer & Wanntorp, 1978; Eldredge & Cracraft, 1980; Wiley, 1981). Cladistics requires that a classification recognize only monophyletic groups (groups that include all and only the descendants of a common ancestor) and hence be isomorphic with the hypothetical genealogy of the taxa. Monophyletic groups can only be recognized on the basis of shared uniquely derived character states (synapomorphies); shared primitive or ancestral character states (symplesiomorphies) can only define paraphyletic groups (those that include some but not all of the descendants of an ancestor). The most compelling argument for adoption of phylogenetic systematics and for using cladistic hypotheses as the basis for classification is that a common genealogy is the sole factor that unites all organisms.

A cladistic analysis of the 19 Central American species of *Heliconia* with pendent inflorescences (hereafter referred to as "pendent species") was undertaken in an attempt to answer two questions: 1) What are the genealogical relationships of the taxa? 2) Is the group of species with pendent inflorescences monophyletic (i.e., is the pendent inflorescence habit shared by these species a synapomorphy that defines a monophyletic group)? The first question can be answered by constructing a cladogram for the taxa, as outlined below. A definitive answer to the second question is more difficult to obtain using only the 19 species included in the revision because these species represent a subset

TABLE 3. Main sites of pistil and pollen inhibition in species of *Heliconia* crossed at Las Cruces Tropical Botanical Garden.*

SPECIES	MAIN SITE OF INHIBITION	
	Pistil	Pollen
<i>H. colgantea</i>	Stigma	Stigma
<i>H. danielsiana</i>		
<i>H. pogonantha</i>		
<i>H. collinsiana</i>	Stigma	Stigma/style
<i>H. nutans</i>		
<i>H. curtispatha</i>	Stigma/style	Stigma
<i>H. mariae</i>		
<i>H. stilesii</i>		
<i>H. trichocarpa</i>	Stigma/style	Stigma/style

*Table from Kress, 1983b, © Annals of Botany Company, 1983; reprinted with permission.

of all heliconias. To provide at least a tentative answer to this question, five species with erect inflorescences (hereafter referred to as “erect species”) were added to the phylogenetic analysis of the pendent species. If either inflorescence habit is uniquely derived in *Heliconia*, then it should define a monophyletic group of species, all of which have that inflorescence type.

METHODS, TAXA, AND CHARACTERS

The basic methodology of phylogenetic systematics includes definition and delimitation of monophyletic taxa as operational units for the analysis; careful and accurate assignment of character states to taxa based upon sound hypotheses of homology; formulation of hypotheses of character-state polarity using outgroup comparison; construction of a cladogram of the taxa; careful mapping of character-state changes on the cladogram and reassessment of the original hypotheses of monophyly, homology, and polarity; and, if appropriate, devising a hierarchical classification based on the monophyletic groups defined by the cladogram.

The results of phylogenetic systematic studies are only meaningful if the taxa under investigation are monophyletic (Hennig, 1966; Eldredge & Cracraft, 1980; Arnold, 1981; Wiley, 1981). It is normally assumed that species are monophyletic. In the present analysis each of the species used as a unit taxon for construction of the cladograms has a suite of apomorphies that suggests it is a monophyletic lineage (see individual species descriptions). The monophyly of the entire group is a central question of the investigation. The presence of a pendent inflorescence in all of the species suggests that the 19 Central American species as a group may be a monophyletic lineage. If the pendent inflorescence is a uniquely derived character in *Heliconia*, the exclusion of all South American pendent species automatically makes it likely that the group is paraphyletic. Nonetheless, the limitations that result from not including all members of a monophyletic group in a phylogenetic analysis do not invalidate the

cladogram as the best hypothesis of relationships of the included taxa. The first cladogram presented here, which includes only the Central American species with pendent inflorescences, therefore provides a testable hypothesis of the genealogical relationships of these taxa.

To test the hypothesis of monophyly of the pendent species, a second cladogram incorporating five additional species with erect inflorescences was constructed. These particular five species were chosen for several reasons. Comparative data on character-state distribution (especially information on pollen characters) were available for the species. The five species are representatives of both of Griggs's (1915) subgenera (*Taeniostrobis* and *Stenochlamys*) and three of his five unranked supraspecific groups that contain erect species (*Imbricatae*, *Distantes*, and *Cannoideae*). The majority of the pendent species fall into his sixth supraspecific taxon, *Pendulae*. *Heliconia imbricata* and *H. wagneriana*, together with *H. mariae* and *H. curtispatha* (with pendent inflorescences), were classified in Griggs's *Imbricatae*, a group of species with imbricate or overlapping cincinnal bracts. *Heliconia wagneriana* has most recently been included by Andersson (1981) in sect. *HELICONIA*, which contains members of Griggs's *Imbricatae* and *Champneianae*. *Heliconia latispatha* and *H. tortuosa* were members of Griggs's *Distantes*, a group of species with erect inflorescences and a *Musa*-like shoot habit. The latter species is very similar to *H. secunda* (with a pendent inflorescence) and therefore suggests some affinity between pendent and erect species (Stiles, 1979). *Heliconia mathiasiae*, although not yet described when Griggs developed his classification, would have been included in his *Cannoideae* because of its "cannoid" (here called *Zingiber*-like) shoot habit. The morphological diversity of the five erect species and their representation of most of Griggs's supraspecific groups of *Heliconia* insures that a reasonable sample of different species was chosen to test the hypothesis of the monophyletic status of the pendent species.

If synapomorphies could easily be recognized and distinguished from similarity due to homoplasy or plesiomorphy, delimitation of monophyletic groups would be simple and unambiguous. The fact that accurate identification of synapomorphies is difficult requires careful and explicit character analysis, especially with regard to comparison of homologous structures. The only phylogenetically useful concept of homology is genealogical: two taxa share a feature because it was present in their common ancestor (Eldredge & Cracraft, 1980). The hypotheses of homology required to construct a cladogram, however, must initially be based on indirect sources of evidence (e.g., similarity in position, anatomy, or development). The resulting cladogram, representing the largest nested set of mutually consistent, hierarchically correlated characters, will then provide a test of these hypotheses of homology. Characters not consistent with the cladogram (those requiring multiple independent origins or reversals) are homoplasious and suggest that the initial hypotheses of homology for these characters were incorrect and in need of reevaluation.

Character states assigned to each of the species (see TABLE 4) for the 30 characters used in the analysis were determined for at least three individuals per population for one to several populations throughout the geographic range of each taxon (TABLE 5). Discrete, nonoverlapping states for characters with

potentially continuous distributions (e.g., overall height, inflorescence size) were determined by the use of bar graphs. Whenever possible, intraspecifically variable characters were eliminated from the analysis. In some cases in which a species was variable for a given character, the state present in its closest relatives was chosen as the primitive state for the variable species. These characters were then reevaluated after the cladogram was constructed. For example, the four varieties of *Heliconia pogonantha* vary in the presence of hairs on the inflorescence. The velutinous perianth present in all varieties of this species is also found in other closely related heliconias that have velutinous to woolly inflorescences. A hairy inflorescence was therefore chosen as the primitive state in the variable *H. pogonantha*.

Outgroup comparison, the most logically justifiable method for determining character-state directionality (Lundberg, 1972; Eldredge & Cracraft, 1980; Stevens, 1980; Watrous & Wheeler, 1981), was used to polarize the characters in *Heliconia* (see TABLE 6). By general consensus (TABLE 2; Baker, 1893; Lane, 1955; Tomlinson, 1962; Dahlgren & Clifford, 1982), members of the "banana-like" families of the Zingiberales, especially the Musaceae and Strelitziaceae, are considered to be the closest relatives of *Heliconia*. Several shared features of floral morphology unite the Heliconiaceae most closely with the Musaceae, and a recent attempt to construct a phylogeny of the entire order (Dahlgren & Rasmussen, 1983) recognizes these two families as sister groups. For the cladistic analyses of *Heliconia*, the two genera of the Musaceae *sensu stricto*, *Musa* and *Ensete*, were chosen as the outgroup. Information on character states in the Musaceae was taken from Lane (1955), Tomlinson (1962), Erdtman (1966), Argent (1976), Dahlgren and Clifford (1982), and Kress and Stone (unpubl.). Character states universally present in this family were scored as primitive in *Heliconia*. Characters not present in the outgroup (e.g., hummingbird pollination), or present with more than one state (e.g., inflorescence habit), were not used. Multistate characters were coded as either unidirectional ($0 \rightarrow 1 \rightarrow 2$; characters 8, 12, 17–21, 24, 25) or bidirectional ($0 \leftarrow 1 \rightarrow 2$; characters 7, 10, 11, 13) according to indirect evidence for character-state homologies (see TABLE 6). For clarity, autapomorphies for single species of *Heliconia* and character states present in the genus but not in the species with pendent inflorescences were also eliminated. In total, the 30 characters used in the analysis contained 44 character-state changes or evolutionary steps (TABLE 6).

The cladogram was constructed using Farris's Wagner '78 computer program. The program is based on a Wagner tree algorithm (Kluge & Farris, 1969; Farris, 1970) that produces the most parsimonious tree without placing any restrictions on homoplasious evolution. One problem with the program is that it may produce cladograms of different lengths depending on the order in which the taxa appear in the data file (Coombs *et al.*, 1981). However, in these analyses the same cladograms were produced regardless of the order in which the taxa were submitted.

RESULTS

CLADOGRAMS. The cladogram of the 19 species with pendent inflorescences (cladogram I; FIGURE 6), including a hypothetical ancestor having all hypoth-

TABLE 4. Taxon by character matrix for 24 species of Heliconia and 30 characters.

Taxon	Character*																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
ANC [†]	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CLG ^{††}	1	0	0	1	1	1	0	2	0	0	1	3	0	1	1	1	1	1	2	0	2	0	0	1	0	1	0	0	0	0
COL	0	1	0	0	0	1	0	1	0	1	1	1	1	1	1	0	1	2	1	1	0	0	0	2	1	1	1	1	0	0
CUR	0	0	0	0	0	0	0	0	1	0	0	2	1	0	0	0	1	1	1	0	1	0	0	2	0	1	1	0	1	0
DAN	0	0	1	0	0	0	2	0	1	2	2	3	2	0	0	0	0	0	2	2	0	1	0	2	2	0	1	0	1	1
IMB	0	0	0	0	0	1	1	0	1	1	1	3	1	1	0	0	1	1	1	1	0	0	1	2	1	0	1	1	0	0
LAT	1	0	0	0	0	1	1	1	0	1	1	1	1	0	0	0	2	2	2	1	0	0	1	2	2	1	1	1	0	0
MAC	1	0	0	1	1	1	1	2	0	1	1	3	1	1	0	1	1	1	2	0	1	0	0	1	0	1	0	0	0	0
MAG	0	0	1	0	0	0	2	0	1	2	2	3	2	0	0	0	0	0	1	2	0	1	0	2	2	0	1	0	1	1
MAR	0	0	0	0	0	0	1	0	0	1	1	2	0	0	0	0	1	1	2	2	1	1	0	2	2	0	1	0	1	1
MAT	0	0	0	0	1	1	1	2	0	1	1	1	1	1	0	0	1	1	2	0	2	0	0	1	0	1	0	0	0	0
MRG	1	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	1	1	2	1	0	0	0	2	1	1	1	1	0	0
NEC	0	0	0	1	1	1	0	1	0	1	1	3	1	1	1	0	1	1	2	0	2	0	0	1	0	1	0	0	0	0
NUT	1	0	0	0	0	1	0	1	0	1	1	1	1	1	0	0	2	2	1	1	0	0	1	2	1	1	1	1	0	0
PLT	1	1	0	0	0	1	0	1	0	0	0	1	1	1	0	1	0	2	1	1	0	0	1	2	1	1	1	1	0	0
POG	0	0	0	0	0	0	2	0	1	2	2	3	2	0	0	0	0	0	2	2	0	1	0	2	2	0	1	0	1	1
RAM	0	0	1	0	0	0	2	0	1	2	2	3	2	0	0	0	0	0	2	2	0	1	0	2	2	0	1	0	1	1
SEC	1	0	0	0	0	1	1	1	0	1	1	1	1	1	0	0	2	2	2	1	0	0	1	2	1	1	1	1	0	0
SES	0	0	0	0	0	0	0	0	1	1	1	3	1	0	0	0	1	1	2	1	1	0	0	2	2	0	1	0	1	1
STI	0	0	0	0	0	0	1	0	1	0	0	2	1	0	0	0	1	1	1	0	1	0	0	2	0	1	1	0	1	0
TAL	0	0	0	1	1	1	1	2	0	1	1	3	0	1	1	1	1	1	2	0	1	0	0	1	0	1	0	0	0	0
TOR	1	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	2	2	1	1	0	0	1	2	1	1	1	1	0	0
TRI	1	0	0	1	1	1	0	2	0	0	1	3	1	1	1	1	1	1	2	0	2	0	0	1	0	1	0	0	0	0
WAG	1	0	0	0	0	1	1	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	2	1	0	1	1	0	0
XAN	0	0	1	0	0	0	2	0	1	2	2	3	2	0	0	0	0	0	1	2	0	1	0	2	2	0	1	0	1	1

*See Table 6 for character states and polarity.
[†]Hypothetical ancestor having all primitive character states.
^{††}For species abbreviations see Table 5.

TABLE 5. Field collections of *Heliconia* species from which character-state data were taken for phylogenetic analyses and descriptions of taxa.

TAXON*	COLLECTION DATA†
<i>H. colgantea</i> Daniels & Stiles (CLG)	Costa Rica: Puntarenas, 77-878
<i>H. collinsiana</i> Griggs (COL)	
var. <i>collinsiana</i>	Guatemala: Alta Verapaz, 77-747 Esquintla, 77-753 Nicaragua: Managua, 77-758
var. <i>velutina</i> Kress	Guatemala: Quezaltenango, 77-756
<i>H. curtispatha</i> Petersen (CUR)	Costa Rica: Limón, 77-789 Nicaragua: Zelaya, 77-759 Panama: Panamá, 77-864
<i>H. danielsiana</i> Kress (DAN)	Costa Rica: Puntarenas, 77-821 San José, 79-1097
** <i>H. imbricata</i> (Kuntze) Baker (IMB)	Costa Rica: Heredia, 79-1101
** <i>H. latispatha</i> Bentham (LAT)	Costa Rica: Heredia, 79-1100
<i>H. maculata</i> Kress (MAC)	Panama: Colón, 80-1240
<i>H. magnifica</i> Kress (MAG)	Panama: Panamá, 77-850, 80-1246
<i>H. marginata</i> (Griggs) Pittier (MRG)	Costa Rica: Puntarenas, 77-804, 79-1095
<i>H. mariae</i> J. D. Hooker (MAR)	Guatemala: Petén, 77-743 Alta Verapaz, 77-745 Costa Rica: Alajuela, 77-771 Heredia, 79-1104 Limón, 77-794 Nicaragua: Zelaya, 77-761 Panama: Canal Zone, 77-855
** <i>H. mathiasiae</i> Daniels & Stiles (MAT)	Costa Rica: Heredia, 79-1105
<i>H. necrobracteata</i> Kress (NEC)	Panama: Coclé, 77-842, 80-1158
<i>H. nutans</i> Woodson (NUT)	Panama: Chiriquí, 77-822, 79-1088, 79-1089a, 79-1089b, 82-1344, 82-1345, 82-1355, 82-1368 Veraguas, 82-1410
<i>H. platystachys</i> Baker (PLT)	Costa Rica: Puntarenas, 77-803 Panama: Canal Zone, 77-860
<i>H. pogonantha</i> Cuf. (POG)	
var. <i>pogonantha</i>	Costa Rica: Heredia, 77-778, 79-1102 Nicaragua: Zelaya, 77-760
var. <i>holerythra</i> Daniels & Stiles	Costa Rica: Limón, 77-790 Panama: Colón, 77-874
var. <i>pubescens</i> Daniels & Stiles	Costa Rica: Cartago/Limón, 77-788
var. <i>veraguasensis</i> Kress	Panama: Veraguas, 77-825
<i>H. ramonensis</i> Daniels & Stiles (RAM)	
var. <i>ramonensis</i>	Costa Rica: Alajuela, 77-764
var. <i>glabra</i> Kress	Panama: Coclé, 83-1589
var. <i>lanuginosa</i> Kress	Panama: Chiriquí, 83-1600, 83-1602
var. <i>xanthotricha</i> Kress	Panama: Coclé, 77-840, 80-1161

TABLE 5 (continued).

TAXON*	COLLECTION DATA†
<i>H. secunda</i> R. R. Smith (SEC) var. <i>secunda</i>	Costa Rica: Heredia, 77-773, 77-776
var. <i>viridiflora</i> Daniels & Stiles	Costa Rica: Guanacaste, 80-1216
<i>H. sessilis</i> Kress (SES)	Panama: Colón, 77-871, 80-1241
<i>H. stilesii</i> Kress (STI)	Costa Rica: Puntarenas, 79-1096 San José, 77-799
<i>H. talamancana</i> Daniels & Stiles (TAL)	Costa Rica: Limón, 77-791
** <i>H. tortuosa</i> Griggs (TOR)	Costa Rica: Puntarenas, 78-944
<i>H. trichocarpa</i> Daniels & Stiles (TRI)	Costa Rica: Alajuela, 77-767, 77-804 Cartago, 77-787 Heredia, 79-1109 Panama: Veraguas, 77-832
** <i>H. wagneriana</i> Petersen (WAG)	Panama: Colón, 80-1244
<i>H. xanthovillosa</i> Kress (XAN)	Panama: Panamá, 80-1233, 83-1565

*Abbreviations for species names used in phylogenetic analysis are given in parentheses following the author. Species with erect inflorescences are indicated by a double asterisk (**).
†All collections were made by the author and are deposited in the Duke University Herbarium (DUKE). For complete locality information, see "Specimens Examined" under the appropriate species description.

esized plesiomorphic character states, had a total length of 84 evolutionary steps. Forty steps were homoplasious. The index of consistency (Kluge & Farris, 1969), which is the total length of the cladogram minus the homoplasies divided by the total length, was .524. This index permits comparisons of the degree of homoplasy or parsimony between cladograms constructed from different character sets or containing different taxa. Character-state changes for each of the 30 characters are indicated on the cladogram.

The second cladogram (cladogram II; FIGURE 7), which includes the 19 pendent and the five erect species, had a total length of 96 steps. Fifty-two steps were homoplasious, and the index of consistency was .458. The same basic topology of the four monophyletic groups of pendent species present in cladogram I was maintained in cladogram II. The five erect species do not form a monophyletic lineage. Three of the erect species are intercalated within pendent lineages: *Heliconia mathiasiae* in the *trichocarpa* group, and *H. latispatha* and *H. tortuosa* in the *nutans* group. The remaining two erect species, *H. wagneriana* and *H. imbricata*, constitute two single-species monophyletic groups that do not share a most recent common ancestor.

CHARACTER ANALYSIS. Twenty of the 30 characters used in the construction of cladogram I had at least one uniquely derived state (characters 2–5, 7–13, 20, 22–25, 27–30). Some characters, such as overall height (character 1) and pollen-grain shape (characters 19, 21), were homoplasious and not phylogenetically

TABLE 6. Thirty characters used in the phylogenetic analyses.

CHARACTER	CHARACTER STATES (values)
1. Overall shoot height	>4 m (0)* <4 m (1)
2. Pseudostem surface	not glaucous (0)* glaucous (1)
3. Pseudostem vestiture	absent (0)* present (1)
4. Leaf-blade shape	oblong-elliptic (0)* oblanceolate (1)
5. Shoot aspect	erect (0)* horizontal/oblique (1)
6. Inflorescence size (number of bracts)	large (>20) (0)* small (<20) (1)†
7. Rachis vestiture	essentially absent (1)* short hairs (0)† long hairs (2)
8. Cincinnal-bract length/width quotient	<1.4 (0)* 1.5–2.0 (1)† >2.0 (2)
9. Cincinnal-bract margins	straight (0)* involute at base (1)
10. Cincinnal-bract outer vestiture	essentially absent (1)* short hairs (0) long hairs (2)
11. Cincinnal-bract inner vestiture	essentially absent (1)* short hairs (0) long hairs (2)
12. Flower shape	straight (0)* slightly curved (1) parabolic (2)† sigmoid (3)
13. Vestiture at perianth apex	essentially absent (1)* short hairs (0) long hairs (2)
14. Anther orientation	connivent inside perianth apex (0)* flared outside perianth apex (1)†
15. Staminode length	<1 cm (0)* >1 cm (1)
16. Ovary vestiture	absent (0)* short hairs (1)
17. Pollen polar diameter	≥60 μm (0)* 49–59 μm (1)† ≤48 μm (2)
18. Pollen equatorial diameter	≥80 μm (0)* 65–79 μm (1)† ≤64 μm (2)
19. Overall pollen shape (P/E)	oblate-spheroidal (≥.88) (0)* suboblate (.76–87) (1) euoblate (≤.75) (2)†

TABLE 6 (continued).

CHARACTER	CHARACTER STATES (values)
20. Pollen polarity (DR/PR)	isopolar (<2) (0)* subisopolar (2–5) (1) heteropolar (>5) (2)
21. Pollen distal-hemisphere shape I	convex (0)* subconvex (1)† planar (2)
22. Pollen distal-hemisphere shape II	not truncate (0)* truncate (1)
23. Pollen distal-hemisphere shape III	not constricted (0)* constricted (1)
24. Pollen distal-hemisphere sculpturing	psilate (0)* granulose–minutely spinulose (1)† spinulose (2)
25. Pollen proximal-hemisphere shape	convex (0)* subconvex (1) planar (2)
26. Pollen proximal-hemisphere sculpturing	psilate (0)* granulose–minutely spinulose (1)†
27. Pollen germination aperture I	indistinct (0)* distinct (1)
28. Pollen germination aperture II	not protruding (0)* protruding (1)
29. Pollen germination aperture III	not sunken (0)* sunken (1)
30. Pollen germination aperture IV	not flattened (0)* flattened (1)

*Character state present in outgroup and originally coded as primitive for *Heliconia*.

†Character state present in most recent common ancestor of species in cladogram I.

informative. Several other features of the pollen grains (characters 22–25, 27–30) proved quite useful in delimiting monophyletic lineages (also see Kress & Stone, 1983). Long hairs on inflorescences and flowers (characters 7, 10, 11, 13) are uniquely derived in one monophyletic group (see below), whereas short hairs appear to have evolved independently in several lineages and are therefore not homologous in all heliconias in which they occur.

The large number of character-state changes (characters 6–8, 12, 14, 17–19, 21, 24, 26) occurring between the hypothetical ancestor and the extant heliconias in cladogram I suggests that the most recent common ancestor of these pendent heliconias did not have some of the originally assigned plesiomorphic states present in the outgroup. These eleven characters were recoded so that the primitive state is the one present not in the outgroup but in the most recent common ancestor (see TABLE 6). In addition, states of multistate characters present in the outgroup but not in the pendent heliconias were eliminated from the transformation series of characters 12, 21, and 24. The result is a more

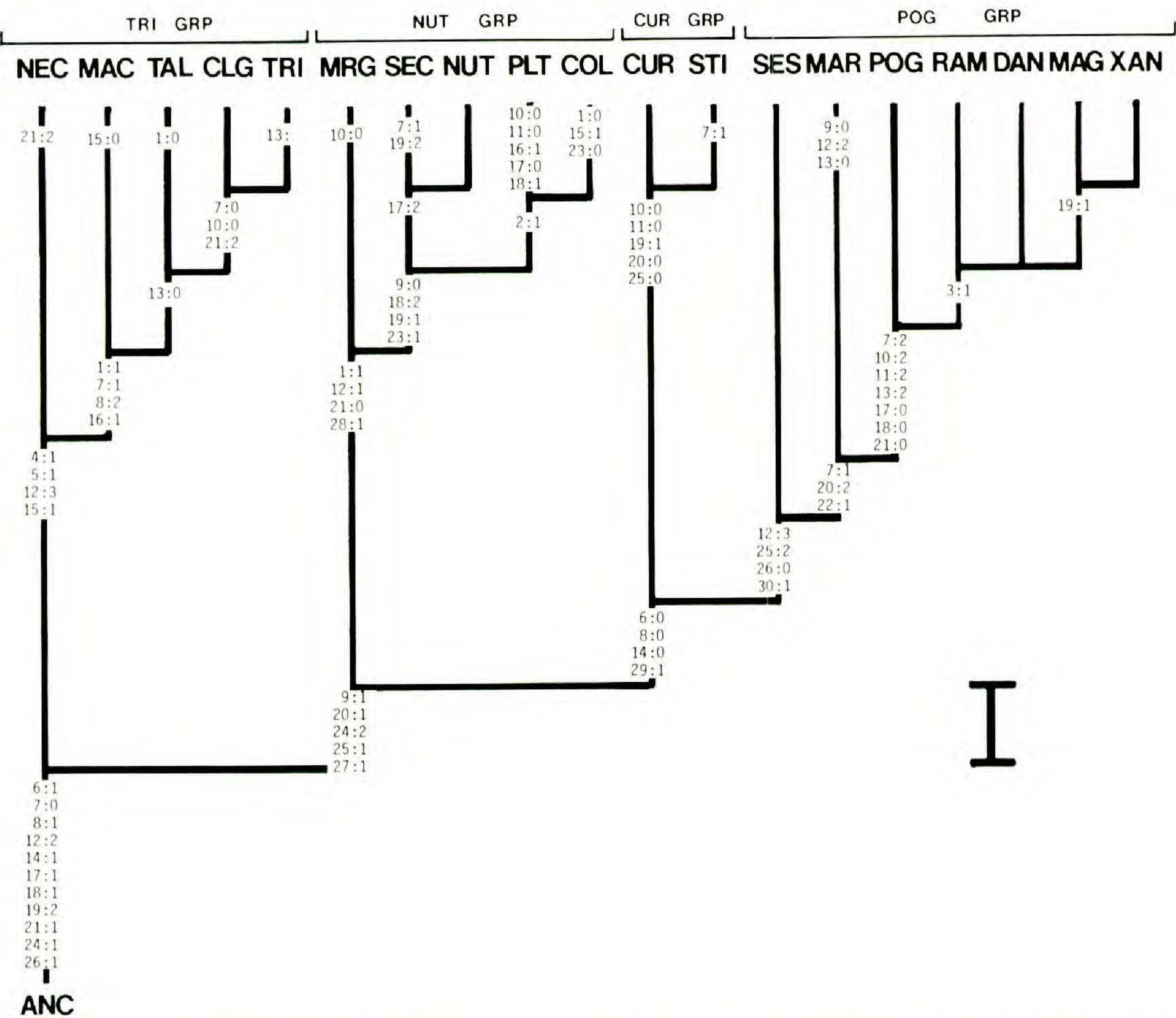


FIGURE 6. Cladogram I. Character-state changes in each lineage given as character number followed by state value. All species have pendent inflorescences. Species groups indicated by horizontal bars above taxa names. (For character states and species abbreviations, see TABLE 6.)

parsimonious cladogram (i.e., with fewer homoplasies) without any alteration in the branching sequence of cladogram I. This revised cladogram (not shown) has eleven fewer homoplasies, six additional synapomorphies (characters 6, 8, 14, 17, 18, 26), and a higher index of consistency (.586). Three characters (7, 19, 21) showed no significant change in homoplasy after the recoding. Although recoding the characters in this fashion does not affect the classification, it does provide new hypotheses on the attributes of the most recent common ancestor of the included pendent species and requires a reevaluation of those character states that are uniquely derived in the various monophyletic lineages. These character-state changes are incorporated into the discussion of monophyletic groups.

MONOPHYLETIC GROUPS. Four primary monophyletic groups or lineages of pendent species are present in both cladograms I and II (FIGURES 6, 7): the *trichocarpa* group (*Heliconia necrobracteata*, *H. maculata*, *H. talamancana*, *H. colgantea*, and *H. trichocarpa*); the *nutans* group (*H. marginata*, *H. secunda*, *H. nutans*, *H. platystachys*, and *H. collinsiana*); the *curtispatha* group (*H.*

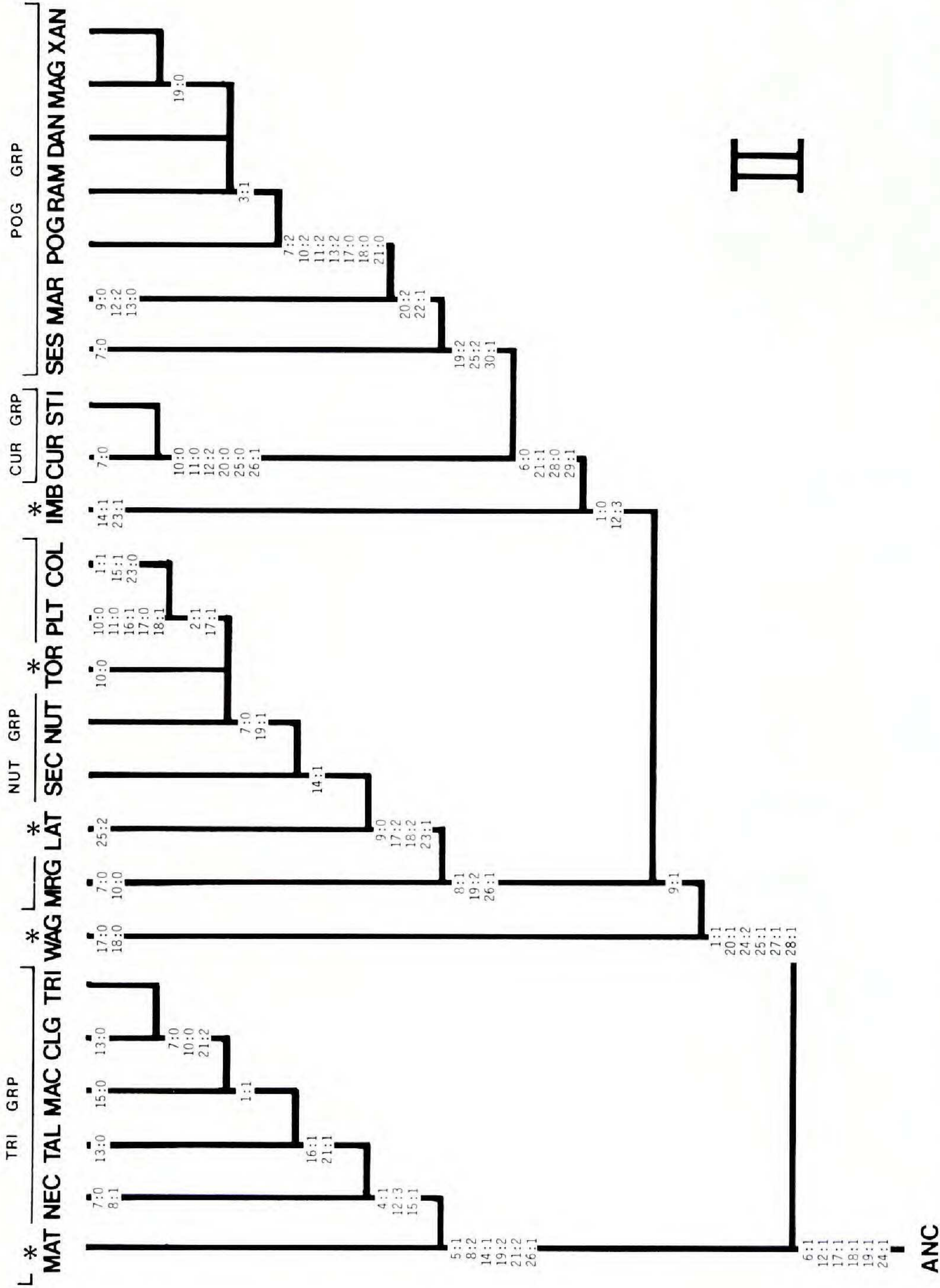


FIGURE 7. Cladogram II. Character-state changes in each lineage given as character number followed by state value. Species with erect inflorescences indicated by an asterisk; all others have pendent inflorescences. Species groups indicated by horizontal bars above taxa names. (For character states and species abbreviations, see TABLE 6.)

curtispatha and *H. stilesii*); and the *pogonantha* group (*H. sessilis*, *H. mariae*, *H. pogonantha*, *H. ramonensis*, *H. danielsiana*, *H. magnifica*, and *H. xanthovillosa*).

The five members of the *trichocarpa* group are united with each other and distinguished from other heliconias by several shared derived character states. Oblanceolate leaves that are widest toward the apex and tapering toward the base, shoots that tend to be held in an oblique or a horizontal plane, and a cincinnal bract l/w quotient greater than 2 (except in *Heliconia necrobracteata*) are synapomorphies of this group. Two pollen characters, granulose to minutely spinulose distal-hemisphere sculpturing and indistinct germination apertures, are unique to this group, but they are also present in the hypothetical ancestor shared by all heliconias. These characters are therefore not synapomorphies but do identify members of the group. Stamínodes over 1 cm long are nearly unique to members of the *trichocarpa* group (except *H. maculata*) but are also present in *H. collinsiana* of the *nutans* group. Similarly, puberulous to tomentose ovaries are primarily found in the *trichocarpa* group (except *H. necrobracteata*) but are also present in a single species of the *nutans* group, *H. platystachys*.

Synapomorphies of the *nutans* group include slightly curved flowers and pollen with protruding germination apertures. Two characters, cincinnal bracts with a l/w quotient between 1.5 and 2, and pollen grains with a subconvex proximal hemisphere, are primarily restricted to the *nutans* group but are also found in its common ancestor with other heliconias and are therefore not synapomorphies. The *nutans* group is more heterogeneous than the *trichocarpa* group. Although *Heliconia marginata* is united by various apomorphies with the other species in this group, it differs in its involute cincinnal bract margins, in its medium-size euoblate pollen grains lacking constricted distal hemispheres, and in several autapomorphies. *Heliconia marginata* may have closer relatives among South American taxa. *Heliconia collinsiana* and *H. platystachys* are united by the presence of a waxy pseudostem, but each has several states unique within the *nutans* group. *Heliconia collinsiana* has large shoots, long staminodes, and pollen grains without a constriction of the distal hemisphere, states that have evolved independently outside the *nutans* group. *Heliconia platystachys* has pubescent cincinnal bracts and ovaries and large pollen grains—characters unique within the *nutans* group but homoplasious within the genus.

The remaining pendent heliconias are members of the sister *curtispatha* and *pogonantha* groups. Large inflorescences with many cincinnal bracts, a cincinnal bract l/w quotient less than 1.5, anthers connivent within the perianth apex, and pollen grains with sunken germination apertures are character states uniquely derived in the common ancestor of these two groups. The *curtispatha* group has no synapomorphies that distinguish it from all other heliconias but does have several unique states that are absent in its sister *pogonantha* group. For example, puberulous to tomentose cincinnal bracts (inner and outer surfaces) and isopolar pollen grains with convex proximal hemispheres are not unique to the *curtispatha* group but distinguish it from the *pogonantha* group.

Several unique pollen-grain features present in the *pogonantha* group are planar, psilate proximal hemispheres and flattened germination apertures. Two

additional pollen-grain character states, heteropolarity and a truncate distal hemisphere, are synapomorphies of the *pogonantha* group minus *Heliconia sessilis*. This latter species is only loosely united with the other species of this group and may represent a Central American species with closer phylogenetic ties to South American taxa not included in this revision. Similarly, *H. mariae* is the sister species to the remaining taxa of the *pogonantha* group, although it has several features (straight cincinnal-bract margins, parabola-shaped flowers, and puberulous perianth apices) that distinguish it from the other members. A velutinous to woolly vestiture on the rachis, cincinnal bracts (outer and inner surfaces), and perianth apices is a synapomorphy of the remaining species (*H. pogonantha*, *H. ramonensis*, *H. danielsiana*, *H. magnifica*, and *H. xanthovillosa*). Large pollen grains (polar diameter greater than 60 μm and equatorial diameter exceeding 80 μm), an additional shared derived feature of these five species, are also independently derived in *H. platystachys* of the *nutans* group. The *pogonantha* group as a whole is more heterogeneous than either the *curtispatha* or the *trichocarpa* group.

EVOLUTION OF THE INFLORESCENCE HABIT. Evidence from cladogram II (FIGURE 7), which was constructed using the original hypotheses on character polarities (TABLE 6), supports the hypotheses that both pendent and erect inflorescences have most likely evolved several times in *Heliconia* and that pendent heliconias do not constitute a monophyletic group. The five species with erect inflorescences do not form a separate monophyletic lineage but are incorporated into several different lineages of pendent species. Synapomorphies supporting the placement of each erect species are indicated on the cladogram.

Inflorescence habit was not used as a character in the construction of cladogram II. Because the outgroup includes species with both pendent and erect inflorescences, the inflorescence habit of the common ancestor of all heliconias is uncertain. According to cladogram II, if the ancestor had an erect inflorescence, the most parsimonious arrangement of state changes of this character requires five evolutionary steps: either three independent origins of pendent inflorescences and two reversals to the erect state, or two separate origins of the pendent state and three reversals to the erect state. If the ancestor had a pendent inflorescence, then five independent origins of the erect habit are required to map the character on the cladogram most parsimoniously. Regardless of the inflorescence type of the common ancestor, this character is very homoplastic in *Heliconia*, and therefore neither state is homologous in all taxa in which it occurs.

DISCUSSION

Before the present investigation of *Heliconia*, few attempts had been made to analyze the phylogenetic relationships within the entire genus or any part of it. Smith (1968), using less than ten characters, constructed a phylogenetic tree for the Middle American species of *Heliconia*, but provided no methodology or rationale to support his conclusions. All of the species with pendent inflorescences were included in a single lineage that excluded all erect species. Stiles (1979, p. 151) placed 37 Costa Rican species into seven groups based

on morphology and phenology and suggested that these groups may correspond to "real evolutionary or taxonomic relationships." He did not state any explicit method by which he formulated his groups, but his decisions have in part been confirmed by the present analyses. Stiles categorized all of the pendent species into two groups, the *pogonantha* group and the *trichocarpa* group. Stiles's *pogonantha* group, corresponding essentially to the *curtispatha* and *pogonantha* groups defined here, would be monophyletic according to cladogram I. As pointed out earlier, the *curtispatha* group has no states uniquely derived within *Heliconia*, and it could therefore be treated as a sublineage within a more broadly defined *pogonantha* group, as was done by Stiles. However, the set of derived character states present in the *curtispatha* group but absent in the *pogonantha* group supports recognition of the separate taxonomic status of the two lineages. Stiles's second pendent group, the *trichocarpa* group, contains species that are here placed in the *trichocarpa* and *nutans* groups and would therefore be paraphyletic according to cladogram I. *Heliconia marginata*, a somewhat aberrant member of the *nutans* group, was listed as *incertae sedis* by Stiles. He further pointed out that some species with pendent inflorescences (e.g., his *trichocarpa* group—especially *H. secunda*) are very similar to some species with erect inflorescences (e.g., his *tortuosa* group), suggesting that all pendent species should not be classified in a single group or even in closely related groups. This suggestion has been substantiated by cladogram II.

Three of the four pendent monophyletic groups discussed in this revision contain some taxa that are not restricted to Central America (e.g., *Heliconia marginata*, *H. platystachys*, *H. curtispatha*, *H. mariae*, and *H. pogonantha*). In addition, each of the four lineages certainly contains one or more South American species not considered here. The heterogeneity of the *nutans* and *pogonantha* groups is probably due to the fact that some of these species (e.g., *H. marginata*, *H. platystachys*, *H. sessilis*, and *H. mariae*), which are quite different from other members of their groups, may have closer relatives in South America than in Central America.

The inclusion of only Central American species requires some caution in the interpretation of the relationships of the taxa in cladograms I and II. However, incorporating pendent South American species or more species with erect inflorescences into the analysis most likely will not require major reinterpretation of the main evolutionary lineages defined here. The addition of more taxa may expand the monophyletic lineages or create new sublineages within the major groups but will not change the relationships among the taxa presently included. For example, *Heliconia mathiasiae*, the sister species of the *trichocarpa* group, has an erect inflorescence and a *Zingiber*-like shoot habit. If other heliconias with *Zingiber*-like shoots were added to the analysis, they would most certainly be placed in the same lineage with *H. mathiasiae*. Taken together, these *Zingiber*-like species would then be the sister group of the *trichocarpa* group. The overall relationships of the other pendent and erect species outside this lineage would not be altered. This reasoning also applies to the inclusion of other species with erect or pendent inflorescences that would be intercalated into the cladogram as sister groups to various species without altering the overall relationships of the other lineages. This was demonstrated here by the incor-

poration of the five species with erect inflorescences in a reanalysis of the pendent species. Neither the relationships of the pendent species nor the circumscription of the four major species groups present in cladogram I was greatly changed in cladogram II by the addition of the extra taxa.

With regard to evolution of inflorescence type, the relatively small number of species included in the cladistic analysis here probably underestimates the degree of homoplasy in this character. An analysis of the entire genus may suggest an even greater number of independent origins of both pendent and erect inflorescences.

CONCLUSIONS

The cladistic analyses support the recognition of at least four separate monophyletic lineages of Central American *Heliconia* with pendent inflorescences. The lineages are here called the *trichocarpa* group, the *nutans* group, the *curtispatha* group, and the *pogonantha* group. The first two groups include some species with erect inflorescences as well. These results suggest multiple independent origins of each inflorescence type and therefore argue against the inclusion of all heliconias with pendent inflorescences in a single monophyletic lineage that excludes all species with erect inflorescences.

SPECIES CONCEPTS

The strong physiological isolating mechanisms that in most cases prevent fertilization between species of *Heliconia* (Kress, 1981b, 1983b) would seem to support the biological species concept (Mayr, 1957, 1969). The many sympatric species of the genus that share habitats, flowering times, and pollinators, as well as the few natural hybrids that are produced, suggest severe restrictions on gene flow between species. Even closely related species (e.g., *H. trichocarpa* and *H. colgantea*; *H. curtispatha* and *H. stilesii*) do not hybridize when artificially cross pollinated. Many *Heliconia* species may indeed be "groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1969, p. 26). This definition of biological species requires reproductive continuity between populations that is mediated through pollen and/or seed dispersal. Experimental evidence for interpopulational gene flow in any species of *Heliconia* is lacking. In the studies on crossability barriers, only tests between species were attempted and no conclusions have been reached concerning crossability between populations of each taxon. For this reason a biological species concept for *Heliconia* is difficult to accept without resorting to *ad hoc* hypotheses on gene flow.

Simpson (1961) and Wiley (1978, 1981) have suggested a species concept that does not rely exclusively on reproductive continuity between populations of a species but does accept it as an important component of species cohesion. The evolutionary species is "a lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley, 1981, p. 25). A lineage consists of one or more populations that share a common history of descent not shared

by other populations. Identity is interpreted as the assemblage of morphological (and behavioral) characters that permits "recognition" between organisms. Reproductive isolation may of course be necessary for maintenance of the genetic identity of an evolutionary species. However, morphological coherence of any species, especially one that is distributed over large geographic areas, is more likely a consequence of genealogy than of gene flow between its members.

Boundaries between species of *Heliconia* were defined by morphological, ecological, and geographic discontinuities. Botanists have variously advocated narrow and broad concepts when awarding species status to recognized taxonomic entities of *Heliconia*. Actually, the taxonomic rank designated by the taxonomist may be of little importance in understanding the biology of the organisms. The duty of the systematist is to document the extent of natural variation, record the levels of discontinuities, and define monophyletic groups. In the present study of *Heliconia*, differences in color, size, and shape of sexual reproductive structures that have been observed in the field have been given high priority in making taxonomic decisions. Assemblages of individuals sharing distinctive cincinnal-bract and flower characteristics that appear to affect pollinator visitation are awarded species status. These morphological characteristics are always correlated with geographic discontinuities. Varietal status is accepted for assemblages of individuals showing minor morphological distinction and allopatric distributions. Taxonomic inflation has been avoided where possible, but not at the expense of obscuring information that is indispensable to other biological investigations.

MATERIALS AND METHODS

The relatively few taxonomic studies of *Heliconia* and the lack of any recent comprehensive revision of the genus are in part due to the difficulties of preparing representative herbarium specimens. Although usually quite common in the Neotropics, heliconias are poorly collected because of their large stature and their fleshy nature, and collections that are made are often unimpressive and uninformative. In preparing the present revision, I have emphasized extensive work with living plants in the field; I have seen all of the taxa described here and have studied them in their natural habitats. Morphological data for the taxonomic descriptions, diagnostic keys, and phylogenetic analysis have been taken from living plants *in situ*, and voucher specimens are deposited in the Duke University Herbarium (DUKE). From one (for the rarer taxa) to seven populations (for the more widely distributed taxa) have been sampled for each taxon (see TABLE 5). Three or more genetically different individuals have been included in each population sample.

In addition to the field studies, numerous specimens from various herbaria (A, BM, CR, DUKE, F, GB, GH, K, M, MO, NY, PMA, S, SCZ, U, UC, US, and w) have been examined. Information from these specimens has been used to supplement field observations on morphology, habitat, geographic distribution, and phenology.

TAXONOMIC TREATMENT

Heliconia L. Mant. Pl. 2: 147. 1771, nom. cons. TYPE SPECIES: *Heliconia bihai* (L.) L.

Bihai Miller, Gard. Dict. abr. ed. 4. Vol. 1 [alph. order]. 1754, nom. rejic.

Bihai Adanson, Fam. Pl. Pt. 2. 67. 1763, nom. rejic.

Heliconiopsis Miq. Fl. Indiae Batavae 3: 590. 1855. TYPE SPECIES: *Heliconiopsis amboinensis* Miq.

Bihaia Kuntze, Rev. Gen. Pl. 2: 684. 1891, orth. var.

Medium to large rhizomatous herbs with *Musa*-, *Canna*-, and *Zingiber*-like habits, forming clones with erect, leafy shoots in groups of few (1 or 2) to many (>50). Pseudostem composed of overlapping sheathing leaf bases of various colors and textures. Leaves usually large, either distichous with all blades lying in a single plane or appearing spirally arranged; petiole short (*Zingiber*-like), medium length (*Canna*-like), or long (*Musa*-like); blade with the base usually unequal on 2 sides of midrib, cordate to attenuate, the upper surface usually green, the lower surface green to maroon. Inflorescence terminal on leafy or leafless shoot, erect, pendent, or nodding, consisting of brightly colored peduncle, rachis, and few (3 to 5) to many (>30) cincinnal bracts; cincinnal bracts distichous or spirally arranged, each subtending cincinnus of few (3) to many (>40) flowers. Flowers hermaphroditic, each subtended by opaque or membranous, variously colored floral bract, persistent or decomposing after anthesis; pedicel short (5 mm) to long (2 cm); perianth consisting of 2 whorls united at base with various degrees of fusion within and between whorls, the calyx with 2 free abaxial sepals adnate to corolla except at apex, and 1 nearly free adaxial sepal usually reflexed at anthesis, the corolla with 3 petals, connate except for free margins opposite free sepal; pollen-bearing stamens 5, the filaments long, linear, attached to base of perianth tube, the anthers 4-loculate, linear, situated at apex of perianth at anthesis, dehiscence longitudinal; pollen large, pseudoinaperturate, oblate to spheroidal, heteropolar with reduced surface ornamentation; staminode 1, opposite free sepal, varying in size and shape; ovary inferior, 3-celled, the ovules solitary, erect, the style filiform, straight, or geniculate, the stigma capitate or lobed. Fruits 1- to 3-seeded drupes, usually blue. Seeds surrounded by stony, roughened endocarp, exarillate; embryo straight; endosperm copious.

KEY TO CENTRAL AMERICAN SPECIES OF HELICONIA WITH
PENDENT INFLORESCENCES

The following key was constructed from living plants and hence is most useful in the field. If sufficient label data are supplied on herbarium sheets, however, the key can be used to identify dried specimens as well. Some characters (e.g., pollen-grain features) will be of limited diagnostic value to most workers, but they are included for completeness. The key is based primarily on the phylogenetic tree (FIGURE 6) and is therefore a "natural" one that reflects the phylogenetic history of the taxa. Members of each of the four species groups

(*trichocarpa*, *nutans*, *curtispatha*, and *pogonantha* groups) are placed together in adjacent entries.

- A. Inflorescences small (< 20 cincinnal bracts); cincinnal bract l/w > 1.4; anthers flared outside perianth apex; pollen germination apertures indistinct or distinctly protruding but not sunken.
- B. Shoots oriented horizontally or obliquely; leaves oblanceolate, widest toward apex and tapering toward base; flowers sigmoid; pollen germination aperture indistinct.
- C. Cincinnal bract l/w < 2; ovaries glabrous. 1. *H. necrobracteata*.
- C. Cincinnal bract l/w > 2; ovaries puberulous to villous.
- D. Rachis and floral bracts usually glabrous; perianth green or yellow-green, slightly sigmoid; staminode apex acuminate or apiculate.
- E. Shoots < 3 m in height; pseudostem pale green with dark brown spots; cincinnal bracts red, becoming green distally; perianth glabrous, yellow, becoming green distally. 2. *H. maculata*.
- E. Shoots usually > 3 m in height; pseudostem green; cincinnal bracts mostly green; perianth puberulous, mostly green. 3. *H. talamancana*.
- D. Rachis and floral bracts puberulous to tomentose; perianth yellow, strongly sigmoid; staminode apex bilobed.
- F. Cincinnal bracts bright pink, often becoming green toward apex, puberulous; floral bracts stiff, conspicuous; perianth puberulous. 4. *H. colgantea*.
- F. Cincinnal bracts red, often becoming maroon toward apex, glabrous; floral bracts soft, inconspicuous; perianth glabrous. 5. *H. trichocarpa*.
- B. Shoots usually erect; leaves oblong-elliptic, widest in middle; flowers only slightly curved; pollen germination aperture distinct and protruding.
- G. Shoots < 3 m in height; pseudostem and lower surface of leaf blade usually not glaucous.
- H. Habitat aquatic; leaves held stiffly erect; cincinnal bracts red and yellow, margins involute at base; staminode apex apiculate; pollen with distal hemisphere lacking constrictions. 6. *H. marginata*.
- H. Habitat terrestrial; leaves not held stiffly erect; cincinnal bracts entirely red, margins straight to revolute at base; staminode apex trilobed; pollen with distal hemisphere having constrictions.
- I. Rachis glabrous, extremely twisted, making inflorescence appear very contorted; perianth length 5–6 cm. 7. *H. secunda*.
- I. Rachis puberulous to tomentose, sometimes twisted so that all cincinnal bracts oriented on one side of inflorescence; inflorescence usually not highly contorted; perianth length 4–5 cm. 8. *H. nutans*.
- G. Shoots > 3 m in height; pseudostem and lower surface of leaf blade usually glaucous.
- J. Cincinnal bracts red and yellow; floral bracts puberulous; ovaries puberulous to tomentose. 9. *H. platystachys*.
- J. Cincinnal bracts entirely red; floral bracts glabrous; ovaries glabrous. 10. *H. collinsiana*.
- A. Inflorescences large (> 20 cincinnal bracts); cincinnal bract l/w < 1.4; anthers connivent within perianth apex; pollen germination aperture distinct but sunken.
- K. Peduncle, rachis, and cincinnal bracts essentially glabrous; flowers parabolic or only slightly sigmoid; perianth essentially glabrous, sometimes slightly puberulous at apex; pollen with distal hemisphere not truncate.
- L. Cincinnal bracts not imbricate, l/w > 0.8; perianth yellow.
- M. Habitat terrestrial; lamina base truncate to cordate; peduncle long, inflo-

- rescence thus distinctly pendent; cincinnal bract l/w 1.1–1.3; flowers parabolic.
- N. Rachis slightly flexuose; cincinnal bracts distichous to spirally arranged, alternate bracts distant and not touching. 11. *H. curtispatha*.
- N. Rachis very flexuose; cincinnal bracts strictly distichous, alternate bracts often touching or overlapping. 12. *H. stilesii*.
- M. Habitat aquatic; lamina base attenuate; peduncle very short, obscure, inflorescence thus sessile and nodding to pendent; cincinnal bract l/w < 1; flowers slightly sigmoid. 13. *H. sessilis*.
- L. Cincinnal bracts imbricate, l/w < 0.9; perianth red to pink. 14. *H. mariae*.
- K. Peduncle, rachis, and/or cincinnal bracts usually densely velutinous to woolly, in some cases all or some parts of inflorescence glabrous; flowers strongly sigmoid; perianth apex densely velutinous; pollen with distal hemisphere truncate.
- O. Peduncle, rachis, and cincinnal bracts essentially glabrous.
- P. Peduncle and rachis red or yellow, cincinnal bracts entirely red or red and yellow; floral bracts and perianth with golden hairs. 15. *H. pogonantha*.
- P. Peduncle, rachis, and cincinnal bracts rose-red; floral bracts and perianth with bright yellow hairs. 16. *H. ramonensis*.
- O. Peduncle, rachis, and/or cincinnal bracts densely velutinous to woolly.
- Q. Cincinnal bracts bichromatic, red and yellow, velutinous. 15. *H. pogonantha*.
- Q. Cincinnal bracts monochromatic, not red and yellow, velutinous to woolly.
- R. Inflorescence orange to rose-red, with orange hairs; perianth with orange or buff to rusty orange hairs.
- S. Inflorescence pink to rose-red, with rusty orange hairs; perianth with rusty orange hairs. 16. *H. ramonensis*.
- S. Inflorescence orange-red with orange (fresh) or buff (dried) hairs. 17. *H. danielsiana*.
- R. Inflorescence burgundy with golden to burgundy hairs or yellow with yellow hairs; perianth with golden or yellow hairs.
- T. Inflorescence deep red to burgundy, with golden to burgundy hairs; perianth with golden hairs. 18. *H. magnifica*.
- T. Inflorescence bright yellow-green with yellow hairs; perianth with bright yellow hairs. 19. *H. xanthovillosa*.

1. ***Heliconia necrobracteata*** Kress, J. Arnold Arbor. **62**: 248. 1981. TYPE: Panama, Coclé, 6 mi beyond El Valle de Antón, behind Cerro Gaital, elev. 900 m, *Kress, Clarkson, & McDade 77-842* (holotype, DUKE!; isotypes, K!, MO!).

FIGURE 8; PLATE I, A, B.

Herb with *Musa*-like habit, 4–4.5 m tall. Leafy shoots in groups of 3 to 12; pseudostem dull gray-green with brown spots, glabrous, 1–2 m tall, 4–6.5 cm in diameter; leaves 3 to 5 per shoot, all tending to lie in horizontal plane; longest petiole olive green, glabrous, 65–100 cm long, 1.5–2 cm in diameter; blade oblanceolate, widest toward acute to obtuse apex, the base unequal, attenuate along petiole, the upper surface dark green, glabrous, with midrib light green and glabrous, the lower surface gray-green, glabrous, with midrib yellow-green and glabrous, the longest blade 1.9–2.4 m by 25–35 cm. Inflorescence pendent, 40–55 cm long; peduncle red, glabrous to puberulous, 25–35 cm long, 1.3–1.8 cm in diameter; rachis flexuose, dark red, puberulous, 1–

1.4 cm in diameter at base; cincinnal bracts spirally arranged, 10 to 20 per inflorescence, oriented 135–140° to axis of inflorescence, becoming more reflexed with age, the basal bract usually fertile, the middle bract with apex acuminate, margins straight, inner surface yellow (sometimes with red margins) and glabrous, outer surface red and glabrous to puberulous, 12–17 cm long, 7–8 cm wide at base, $l/w = 1.9$, all bracts becoming necrotic soon after anthesis, deteriorating distally first and basipetally with age. Floral bracts more or less translucent at anthesis, quickly decomposing, white, puberulous to velutinous along abaxial margins, 3.5–4.5 cm long, 1.5–2 cm wide at base. Flowers 8 to 13 per cincinnus; pedicel pale yellow, tomentose, 1.4–2.2 cm long; perianth yellow to deep yellow, glabrous, puberulous along margins, 4.5–5 cm long, 6–9 mm wide at base, at anthesis curved 50–80° and sigmoid; free sepal reflexed, fused sepals with apices slightly reflexed; staminode white, 1.5–2 cm by 4–5 mm, apex bilobed; stamens with anthers partially flared outside of apex of corolla tube; pollen *trichocarpa* type, medium size ($54 \times 74 \mu\text{m}$), euoblate ($P/E = 0.72$), isopolar ($DR/PR = 1.02$), with the distal hemisphere planar, minutely spinulose, the proximal hemisphere convex, minutely spinulose to granulose, the germination aperture indistinct; ovary pale yellow, glabrous, 5–6 by 6–7 mm. Drupes glabrous.

SPECIMENS EXAMINED. **Panama.** COCLÉ: base of three peaks beyond El Valle de Antón, elev. 800 m, *Kress & Cooper-Smith 76-652* (DUKE); behind Cerro Gaital, elev. 2200 ft, *Kress et al. 80-1158* (DUKE), elev. 2400 ft, *Kress & Hammel 83-1583* (DUKE); mtns. above El Valle, in forest on Sr. Furlon's Finca, *Stimson 5037* (scz), *5038* (scz).

PHENOLOGY. Flowering early in rainy season (April) through late August.

HABITAT AND DISTRIBUTION. This species is found on steep, forested slopes at elevations of 650–1000 m in the region of El Valle de Antón in Panama (MAP 1). As more collections are made in the provinces of Coclé and Veraguas, especially on the Atlantic slopes, the known distribution will probably be broadened.

RELATIONSHIPS. *Heliconia necrobracteata*, a member of the *trichocarpa* group, is distinctive in its glabrous ovaries, its stouter vegetative shoots and inflorescences, and its red cincinnal bracts that decompose and turn black even while flowers are still being produced.

2. ***Heliconia maculata*** Kress, J. Arnold Arbor. **62**: 244. 1981. TYPE: Panama, Colón, along Río Guanche, 1 km from road to Portobelo, elev. ca. 8 m, *Kress & Knapp 80-1240* (holotype, DUKE!; isotypes, F!, GH!, K!, MO!, PMA!).

FIGURE 9; PLATE I, C, D.

Herb with *Musa*-like habit, 2–2.5 m tall. Leafy shoots congested, in groups of 3 to 25; pseudostem pale greenish gray with distinctive dark brown spots throughout, glabrous, 1.2–1.7 m tall, 2.2–2.5 cm in diameter; leaves 6 per shoot, all tending to lie in horizontal plane; petiole olive green, glabrous, 22–34 cm long, 8–10 mm in diameter; blade oblanceolate, widest toward acute apex, the base unequal, attenuate, extending along petiole, the upper surface green, glabrous, with midrib light green and glabrous, the lower surface gray-green, glabrous, with midrib yellow and glabrous to slightly scurfy, the longest

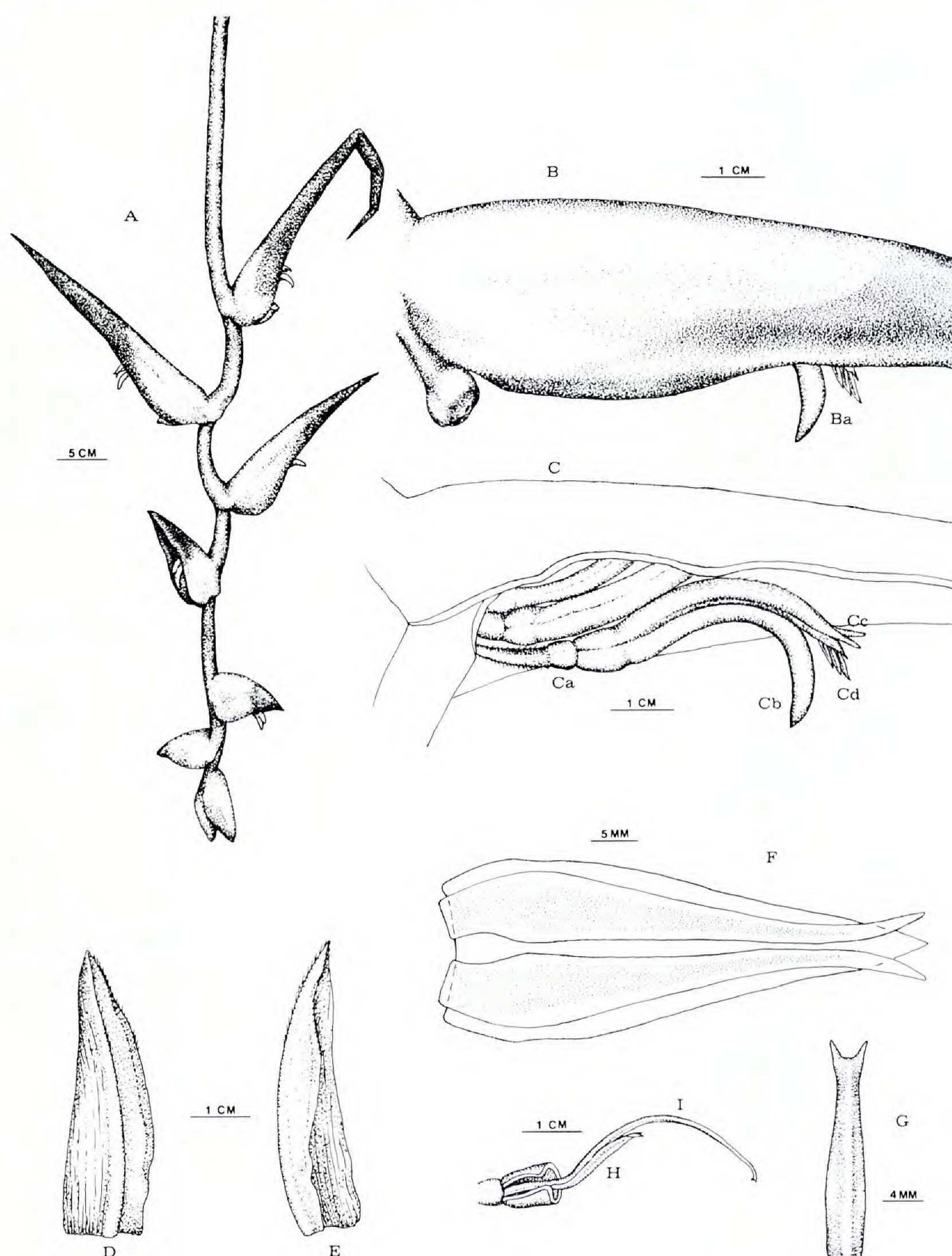
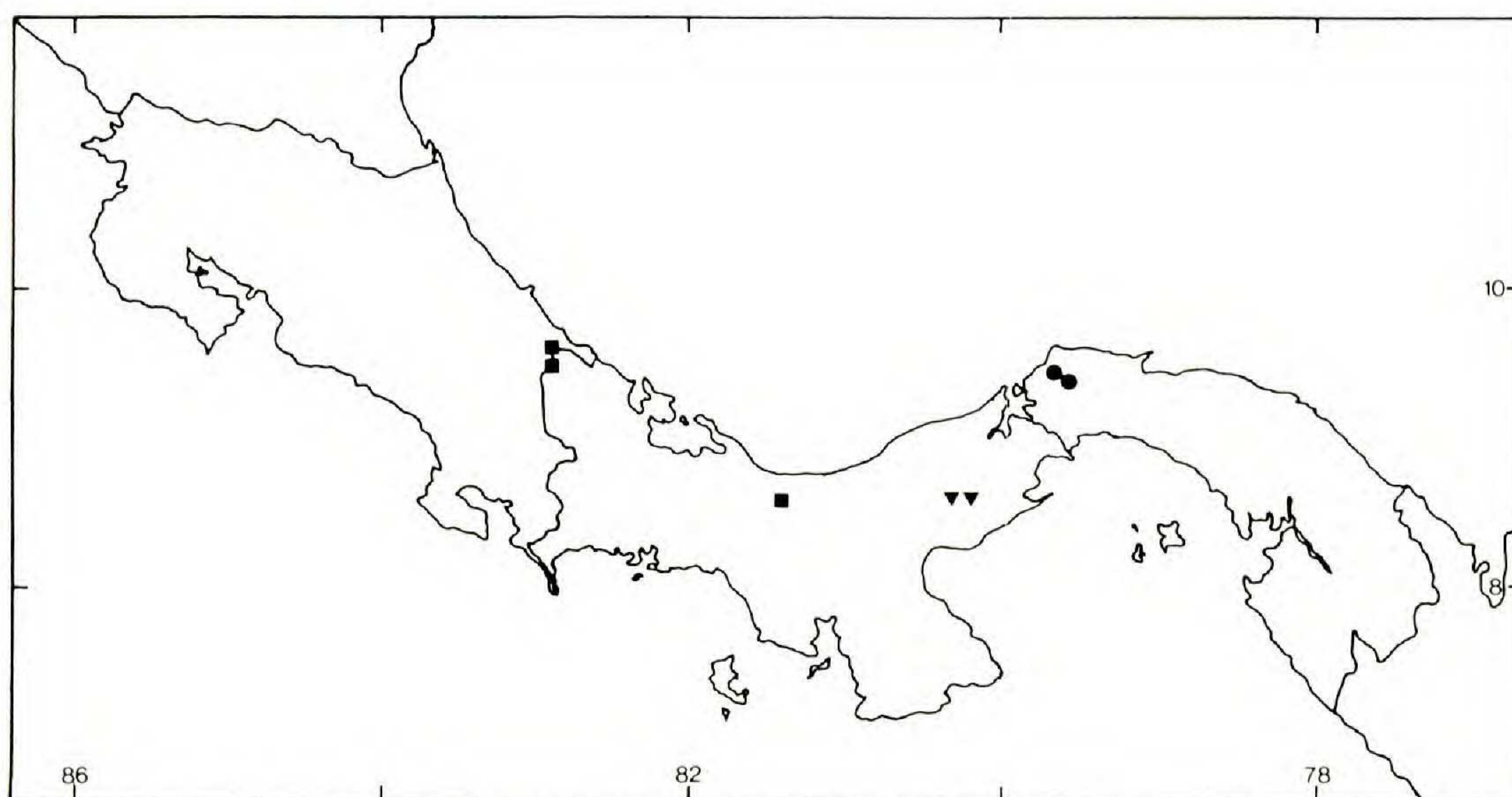


FIGURE 8. *Heliconia necrobracteata*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, slightly reflexed; Cd, anthers, partially exserted). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma.

blade 1.1–1.3 m by 24–26 cm. Inflorescence pendent, to 51 cm long; peduncle green and dark maroon, glabrous, 7–32 cm long, 1 cm in diameter; rachis flexuose, dull red, glabrous to slightly puberulous, 7–8 mm in diameter at base; cincinnal bracts spirally arranged, 7 or 8 per inflorescence, oriented 90° to axis



MAP 1. Costa Rica and Panama, showing allopatric distribution of *Heliconia necrobracteata* (triangles), *H. maculata* (circles), and *H. talamancana* (squares).

of inflorescence, the basal bract fertile or sterile, the middle bract with apex long-acuminate, margins straight becoming somewhat flared at base, inner surface pale orange and glabrous, outer surface red basally becoming green toward apex and glabrous, 14–17 cm long, 4–4.5 cm wide at base, $l/w = 3.7$. Floral bracts translucent at anthesis, quickly decomposing, cream, glabrous to puberulous abaxially, 4–5 cm long, 1.1–1.4 cm wide at base. Flowers 15 to 20 per cincinnus; pedicel pale yellow, pubescent to hirsute, 1–1.5 cm long; perianth yellow basally, green at apex, glabrous to slightly puberulous, 5 cm long, 1 cm wide at base, at anthesis curved 30–50° and slightly sigmoid; free sepal slightly reflexed, fused sepals with apices not reflexed; staminode white, 7–10 by 3 mm, apex apiculate; stamens with anthers flared outside perianth apex; pollen *trichocarpa* type, medium size ($49 \times 67 \mu\text{m}$), euoblate ($P/E = 0.73$), isopolar ($DR/PR = 0.97$), the distal hemisphere subconvex, verrucose, the proximal hemisphere convex, granulose, the germination aperture indistinct; ovary white, pubescent, 4–5 by 6 mm. Drupes glabrous to puberulous, 8 by 9 mm; pyrenes 6 by 5 mm.

SPECIMENS EXAMINED. **Panama.** COLÓN: Río Guanche, forest, elev. ca. 50 ft, *Maas et al.* 1583 (F, MO); in forest 3–7 km from bridge, elev. 300–700 ft, *Hammel et al.* 4899 (MO); *Knapp* 1020 (MO), 1422 (MO); below Cerro Bruja along Río Escondaloso, elev. 100–200 m, *Kress & Knapp* 82-1406 (DUKE).

PHENOLOGY. Flowering late July through early October.

HABITAT AND DISTRIBUTION. This species occurs at lower elevations along stream banks and in adjacent understory of primary forest. It will invade more open areas (often created by man), where it generally produces more shoots per clump. So far, *Heliconia maculata* has been collected at only two localities in Colón Province, Panama (MAP 1); as more collections are made, it will probably be found in other forested areas in the Atlantic coastal forests of Panama.

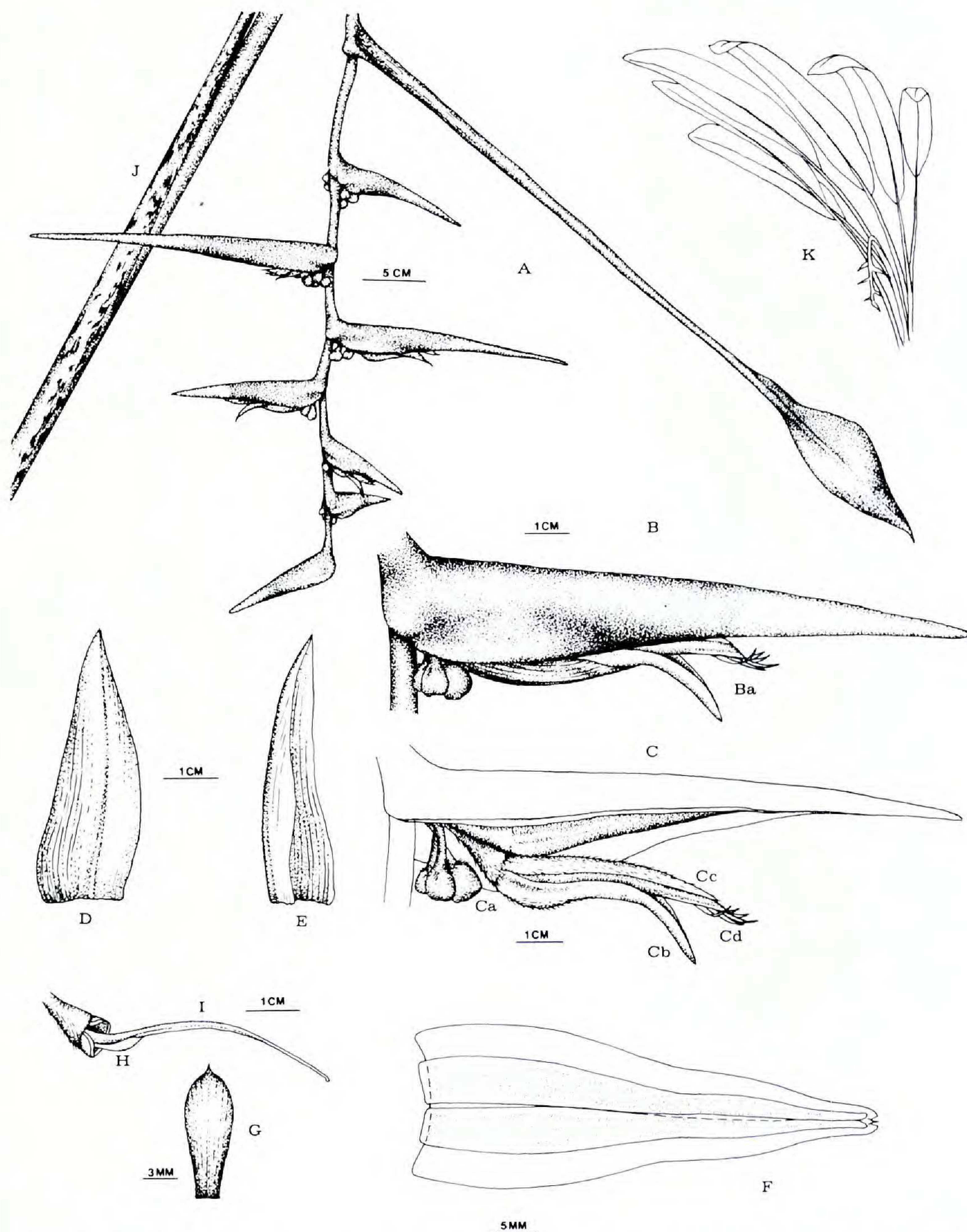


FIGURE 9. *Heliconia maculata*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, not reflexed; Cd, anthers, exerted). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma. J, pseudostem. K, vegetative habit.

RELATIONSHIPS. Several pollen characters, as well as the distinctive pubescent ovaries and the obliquely or horizontally oriented leaf blades that are widest near the apex, ally this species with other members of the *trichocarpa* group. However, it differs from the other species in its dark brown-spotted pseudostem (also present in *Heliconia necrobracteata*), its red and green cincinnal bracts, and its yellow and green, glabrous perianths.

3. ***Heliconia talamancana*** Daniels & Stiles, *Brenesia* **15**(Supl.): 42. 1979. TYPE: Costa Rica, [Limón,] on ridge W of BriBrí, elev. 200 m, *Daniels, Stiles, & Kress 115* (holotype, F!; isotypes, CR, US). PLATE I, E, F.

Herb with *Musa*-like habit, 4–4.5 m tall. Leafy shoots in groups of 5 to 15; pseudostem green, glabrous, 2.2–2.6 m tall, 3.5–4 cm in diameter; leaves 5 per shoot, all tending to lie in horizontal plane; petiole olive green, glabrous, 85–100 cm long, 1.5–1.6 cm in diameter; blade oblanceolate, widest toward obtuse apex, the base unequal, attenuate along petiole, the upper surface green, glabrous, with midrib green and glabrous, the lower surface gray-green, glabrous, with midrib green-yellow and glabrous, the longest blade 2.1–2.5 m by 32–35 cm. Inflorescence pendent, to 65 cm long; peduncle green, glabrous, 6–27 cm long, 1.3–1.5 cm in diameter; rachis flexuose, green and red, glabrous, 1.2–1.4 cm in diameter at base; cincinnal bracts spirally arranged, 8 to 13 per inflorescence, oriented 90° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex long-acuminate, margins straight, inner surface white to green and glabrous, outer surface green becoming red at rachis and glabrous, 17–20 cm long, 6–7 cm wide at base, $l/w = 2.9$. Floral bracts opaque, decomposing after anthesis, white, glabrous to puberulous abaxially, 5–5.3 cm long, 1.5–2 cm wide at base. Flowers 15 to 20 per cincinnus; pedicel white, tomentose, 1.3–1.6 cm long; perianth white, green apically, puberulous, 5–5.2 cm long, 1 cm wide at base, at anthesis curved 30–40° and slightly sigmoid; free sepal reflexed, fused sepals with apices not reflexed; staminode white, spatulate, 1.1 cm by 3 mm, apex apiculate; stamens with anthers partially flared outside corolla tube; pollen *trichocarpa* type, medium size ($53 \times 72 \mu\text{m}$), euoblate ($P/E = 0.74$), isopolar ($DR/PR = 0.95$), with the distal hemisphere subconvex to planar, verrucose to granulose, the proximal hemisphere convex, verrucose to granulose, the germination aperture indistinct; ovary white, villous, 6–8 by 7–8 mm. Drupes puberulous, 1–1.2 by 1.2–1.5 cm.

SPECIMENS EXAMINED. **Costa Rica.** LIMÓN: 1–3 km N of BriBrí, Río Sixaola Drainage, elev. 20–200 m, *Burger & Antonio 11000* (F); in hills above BriBrí, elev. ca. 250 m, *Kress et al. 76-625* (DUKE), elev. ca. 800 ft, *Kress et al. 77-791* (DUKE). **Panama.** VERAGUAS: along road on Pacific slope, 1–3 km above Escuela Agrícola Alto Piedra, elev. 700–800 m, *Croat 25997* (MO).

PHENOLOGY. Flowering June to October.

HABITAT AND DISTRIBUTION. This species is distributed on the Caribbean slopes from the Río Sixaola in Limón, Costa Rica, to Veraguas, Panama (MAP 1). It is most often found on steep, wooded slopes in primary and old secondary growth at elevations up to 700 m.

RELATIONSHIPS. *Heliconia talamancana* is closely related to *H. maculata* and other species in the *trichocarpa* group. It differs from *H. maculata* in its greater overall stature (> 3 m), its essentially green cincinnal bracts, and its green, pubescent perianth.

4. ***Heliconia colgantea*** R. R. Smith ex Daniels & Stiles, *Brenesia* 15(Supl.): 18. 1979. TYPE: Costa Rica, [Puntarenas,] 10 km ENE of Palmar Norte, *Burger & Matta* 4662 (holotype, F!; isotypes, CR!, GH!, NY!, US!).

PLATE II, A, C.

Herb with *Musa*-like habit, 2 m tall. Leafy shoots solitary or in pairs; pseudostem yellow-green, glabrous, 90–125 cm tall, 2.2–2.7 cm in diameter; leaves 6 per shoot, all fanning out from pseudostem and tending to lie in horizontal plane; petiole green to dark green, glabrous, 34–45 cm long, 9–11 mm in diameter; blade oblanceolate, widest toward obtuse apex, the base unequal, obtuse to attenuate along petiole, the upper surface dark green, glabrous, with midrib dark green and glabrous, the lower surface gray-green, glabrous, with midrib green and glabrous, the longest blade 1.1–1.3 m by 20–25 cm. Inflorescence pendent, to 45 cm long; peduncle red with green striations, puberulous, 14–17 cm long, 1–1.2 cm in diameter; rachis flexuose, pink-red, puberulous to tomentose, 9–10 mm in diameter at base; cincinnal bracts spirally arranged, 8 to 10 per inflorescence, oriented $120\text{--}165^\circ$ to axis of inflorescence, becoming more reflexed with age, the basal bract usually fertile, the middle bract with apex acuminate, margins straight becoming somewhat revolute near rachis, inner surface yellow and pink and glabrous, outer surface pink becoming green toward apex and puberulous, 19–22 cm long, 7–8 cm wide at base, $l/w = 2.7$. Floral bracts translucent, persistent, conspicuous, pale yellow, stiff, puberulous abaxially, 3.5–4.2 cm long, 8–10 mm wide at base. Flowers 15 to 20 per cincinnus; pedicel pale yellow, puberulous to tomentose, 1–1.2 cm long; perianth yellow, densely puberulous, 5.1–5.5 cm long, 8–9 mm wide at base, at anthesis curved $50\text{--}70^\circ$ and sigmoid; free sepal reflexed, fused sepals with apices sometimes slightly reflexed; staminode white, 1–1.1 cm by 2–3 mm, apex bidentate; stamens with anthers flared outside perianth apex; pollen *trichocarpa* type, medium size ($55 \times 79 \mu\text{m}$), euoblate ($P/E = 0.69$), isopolar ($DR/PR = 0.88$), with the distal hemisphere planar, minutely spinulose, the proximal hemisphere convex, minutely spinulose to granulose, the germination aperture indistinct; ovary pale yellow, puberulous to tomentose, 4–6 by 6–7 mm. Drupes sparsely tomentose.

SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: forested hills near Palmar Norte, elev. 300 m, *Allen* 6551 (F, PMA); 10 km N of Palmar Norte along Pan Am Hwy., elev. ca. 100 m, *Kress et al.* 76-595 (DUKE), 77-878 (DUKE); cult. at Las Cruces Trop. Bot. Garden, San Vito de Java, elev. 3900 ft, *Kress* 78-1027 (DUKE). **Panama.** CHIRIQUÍ: Burica Peninsula, 10–11 mi W of Puerto Armuelles in vic. of San Bartolo Limite, elev. 300–500 m, *Croat* 21994 (F). DARIÉN: Río Pucuro between Cerro Mali and Cerro Tacarcuna, Río Pucuro base camp, elev. 650 m, *Gentry & Mori* 13877 (MO); E slope of Cerro Sapo, elev. 2500 ft, *Hammel* 1275 (MO); Río Pirre, near Dos Bocas, *Foster & Augsburg* 2844 (F); Cerro Pirre, *Bristan* 628 (NY), 629 (NY); 4.5 km S of El Real, moist forest at base of foothills of N slope of Cerro Pirre, *Mori & Kallunki* 5413 (GB, MO); headwaters of Río

Tuquesa, vic. of gold-mining camp of Tyler Kittredge, *Croat* 27198 (MO); 10 km NE of Jaqué, Río Pavarando, elev. 1400 ft, *D'Arcy & Sytsma* 14522 (MO), *Sytsma & D'Arcy* 3375 (MO); Río Jaqué valley, elev. 300–500 m, *Knapp & Mallet* 3085 (MO). PANAMÁ: S of Ipetí, Serranía de Majé, elev. 450–600 m, *Knapp et al.* 4553 (MO).

PHENOLOGY. Flowering mainly January to September.

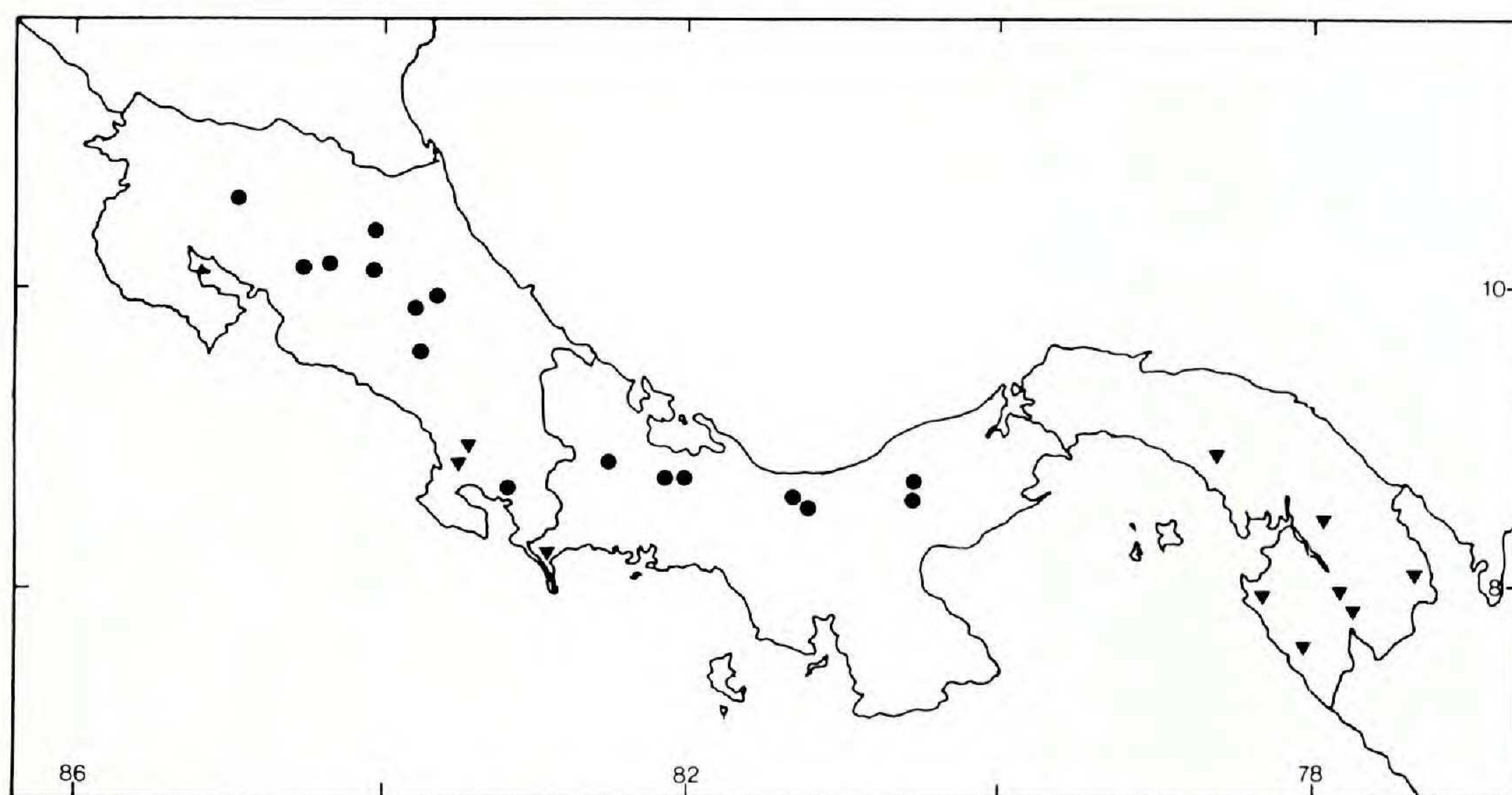
HABITAT AND DISTRIBUTION: *Heliconia colgantea* has been found in several localities in Costa Rica and Panama (MAP 2). It is restricted mainly to moist or wet forested slopes and ravines between 100 and 800 m.

RELATIONSHIPS. This species is a member of the *trichocarpa* group. Slightly pubescent, bright pink cincinnal bracts with green apices, a puberulous perianth, and stiff, conspicuous floral bracts distinguish *Heliconia colgantea* from its closest relative, *H. trichocarpa*.

5. ***Heliconia trichocarpa*** Daniels & Stiles, *Brenesia* 15(Supl.): 44. 1979. TYPE: Costa Rica, Alajuela, La Balsa area N of San Ramón, elev. 800 m, *Daniels, Kress, & Hutchison* 112 (holotype, F!; isotypes, CR, US).
PLATE II, B, D.

H. trichocarpa var. *caducispatha* Daniels & Stiles, *Brenesia* 15(Supl.): 44. 1979. TYPE: Costa Rica, Puntarenas, 42 km S of Palmar Norte along Interamerican Hwy., elev. 100 m, *Daniels & Stiles* 129 (holotype, F!; isotypes, CR, US).

Herb with *Musa*-like habit, 2–4 m tall. Leafy shoots in groups of 4 to 20; pseudostem green (sometimes with red), glabrous, 80–190 cm tall, 2–4 cm in diameter; leaves 4 to 6 per shoot, all tending to lie in horizontal plane; petiole green to olive green, glabrous, 35–90 cm long, 7–13 mm in diameter; blade oblanceolate, widest toward acute to obtuse apex, the base unequal, obtuse to attenuate along petiole, the upper surface green to dark green, glabrous, with midrib light green to olive green and glabrous, the lower surface gray-green, glabrous, with midrib yellow-green and scurfy, the longest blade 85–175 by 17–30 cm. Inflorescence pendent, to 60 cm long; peduncle red to rose-red, puberulous, 10–50 cm long, 1–1.8 cm in diameter; rachis flexuose, red, puberulous, 6–11 mm in diameter at base; cincinnal bracts spirally arranged, 6 to 10 per inflorescence, oriented 110–150° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex long-acuminate, margins straight, inner surface white to yellow to pink and glabrous, outer surface red to rose-red and glabrous to puberulous, 12–28 cm long, 6–8 cm wide at base, l/w = 2.9. Floral bracts translucent, persistent, inconspicuous, white to yellow, soft, puberulous abaxially, 4.5–6 cm long, 1.5–2.5 cm wide at base. Flowers 10 to 20 per cincinnus; pedicel pale yellow, puberulous to tomentose, 7–13 mm long; perianth yellow, glabrous to puberulous, 4.6–5.5 cm long, 1–1.2 cm wide at base, at anthesis curved 50–70° and sigmoid; free sepal reflexed, fused sepals with apices not reflexed; staminode white, 1–1.3 cm by 2–3 mm, apex bidentate; stamens with anthers flared outside perianth apex; pollen *trichocarpa* type, medium size ($53 \times 78 \mu\text{m}$), euoblate ($P/E = 0.68$), isopolar ($DR/PR = 1.07$), with the distal hemisphere planar, minutely spinulose to verrucose, the proximal hemisphere convex, minutely spinulose to granulose, the germination



MAP 2. Costa Rica and Panama, showing distribution of *Heliconia colgantea* (triangles) and *H. trichocarpa* (circles).

aperture indistinct; ovary white to pale yellow, puberulous to tomentose, 5–8 by 6–9 mm. Drupes tomentose.

SPECIMENS EXAMINED. **Costa Rica.** ALAJUELA: entre Cataratas y La Balsa de San Ramón, elev. 700–800 m, *Brenes 4429* (CR, F), elev. ca. 1000 m, *Kennedy 1657* (MO), elev. ca. 800 m, *Kress et al. 76-605* (DUKE), elev. 2700 ft, *Kress et al. 77-767* (DUKE), 77-807 (DUKE), elev. 900–1000 m, *Stevens 13791* (MO); Finca Los Ensayos ca. 11 mi NW of Zarcero, elev. 850 m, *Croat 43597* (MO); Buena Vista de San Carlos, Quebrada Lajas, Finca Los Ensayos, elev. 850 m, *Jiménez 2323* (CR, F, NY); between San Lorenzo and Los Angeles de San Ramón, above Río San Lorenzo, elev. 620 m, *Burger & Antonio 11190* (F); Colonia Virgen del Socorro, barranca of Río Sarapiquí, elev. 700–800 m, *Stevens 13565* (MO). CARTAGO: forêts de Tuis, elev. 650 m, *Tónduz 11383* (CR, US); woods above Río Pejibaye, 2 km SW of Taus, elev. 740 m, *Lent 2986* (F); near Moravia, elev. 1150–1200 m, *Maas 1075* (U). CARTAGO/LIMÓN: between Turrialba and Siquirres, elev. 2000–2500 ft, *Kress et al. 77-787* (DUKE). GUANACASTE: below Volcán Tenorio along road to Upala, elev. 700 ft, *Kress et al. 80-1217* (DUKE). HEREDIA: Finca La Selva near Puerto Viejo de Sarapiquí, elev. ca. 150 m, *Kress 79-1109* (DUKE). LIMÓN: along Hwy. 32 from Turrialba to Limón, 11 mi S of Siquirres, elev. 650 m, *Croat 43350* (MO). PUNTARENAS: 3.5 mi beyond Golfito in primary forest, elev. ca. 25 m, *Kress et al. 76-592* (DUKE); San Vito de Java, cult. at Los Cruces Trop. Bot. Garden, elev. ca. 4000 ft, *Kress 76-572* (DUKE), 78-975 (DUKE). SAN JOSÉ: streamsides along Río Claro Valley (Río La Hondura drainage), below La Palma, NE of San Jerónimo, elev. 1000–1200 m, *Burger & Burger 7657B* (F). **Panama.** CHIRIQUÍ: Fortuna, elev. 1000–1200 m, *Correa et al. 2668* (MO); upriver from main camp, Fortuna Dam Site, 1200–1400 m, *Folsom et al. 5509* (MO); *Kress & Hammel 83-1605* (DUKE). COCLÉ: El Copé, beyond sawmill, elev. 2800 ft, *Kress et al. 80-1171* (DUKE), *Kress & Hammel 82-1323* (DUKE); El Potroso, elev. 800–1000 m, *Andersson & Sytsma 1276* (s), *D'Arcy 11273* (MO). VERAGUAS: valley of Río Dos Bocas on road between Alto Piedra (above Santa Fé) and Calovébora, elev. 350–400 m, *Croat 27429* (MO), elev. 500 m, *Andersson & Sytsma 1286* (GB, s); beyond Santa Fé above Escuela Agrícola, elev. 2600 ft, *Kress & Cooper-Smith 76-657* (DUKE), *Kress et al. 77-832* (DUKE); Atlantic slope beyond Santa Fé on road to Calovébora, elev. 1200

ft, *Kress et al.* 80-1196 (DUKE); Río Calabacito, Aguabal, elev. 400 m, *Maas & Dressler* 1624 (MO, U).

PHENOLOGY. Flowering mainly during late rainy season (July to November), peaking September and October.

HABITAT AND DISTRIBUTION. *Heliconia trichocarpa* is distributed throughout Costa Rica and Panama, primarily on the Atlantic slopes at elevations between 100 and 1000 m (MAP 2). This species is found in a wide range of habitats, from stream margins in primary forest understory to roadside embankments in early secondary growth.

VARIATION. Daniels and Stiles (1979) recognized two varieties of *Heliconia trichocarpa*: var. *trichocarpa* and var. *caducispatha*. They listed several characters by which the two taxa differ, the most important one being the rapid postanthesis disintegration of the cincinnal bracts in the latter variety. Although there are some morphological differences, the extent of variation between varieties is not greater than that between populations of var. *trichocarpa* on the Atlantic slopes. In addition, intermediate forms between varieties are known (e.g., *Kress et al.* 76-592, DUKE). For these reasons var. *caducispatha* is not accepted here.

RELATIONSHIPS. *Heliconia trichocarpa* is allied to other species of the *trichocarpa* group with horizontally oriented oblanceolate leaf blades that are widest toward the apex, smaller pendent inflorescences with long-acuminate cincinnal bracts ($l/w > 2.5$), pubescent ovaries, and pollen with indistinct germination apertures. Its closest relative is *H. colgantea*, from which it differs in its glabrous, red cincinnal bracts, its inconspicuous, decomposing floral bracts, and its glabrous perianth.

6. ***Heliconia marginata*** (Griggs) Pittier, Man. Pl. Usual. Venez. 299. 1926.

PLATE III, A, B.

Bihai marginata Griggs, Bull. Torrey Bot. Club **42**: 323. 1915. TYPE: Panama, [Darién,] Marraganti and vic., *Williams* 696 (holotype, NY!; isotype, US!).

Herb with *Musa*-like habit, 2–3 m tall. Leafy shoots in groups of 20 to over 50; pseudostem gray-green, glabrous, 45–120 cm tall, 4.3–7 cm in diameter; leaves 4 or 5 per shoot, held stiffly erect; petiole green, glabrous, 45–90 cm long, 8–12 mm in diameter; blade with the base unequal, obtuse to attenuate, the apex acuminate, the upper surface green to bright green, glabrous, with midrib green and glabrous, the lower surface green, glabrous to slightly glaucous, with midrib green and glabrous, the longest blade 60–120 by 17–25 cm. Inflorescence pendent, to 40 cm long; peduncle red and green, scurfy, 35–60 cm long, 9–10 mm in diameter; rachis flexuose, red, puberulous to scurfy, 6–12 mm in diameter at base; cincinnal bracts distichous to spirally arranged, 9 to 14 per inflorescence, oriented 90–120° to axis of inflorescence, the basal bract often sterile, the middle bract with apex acute to acuminate, margins straight becoming involute at base, inner surface yellow and glabrous, outer surface red becoming yellow along margins and puberulous, 7–9.5 cm long, 4.5–5.5 cm

wide at base, $l/w = 1.7$. Floral bracts opaque, persistent, yellow and pink, puberulous to villous abaxially, 5–6 cm long, 1.9–2 cm wide at base. Flowers 7 to 15 per cincinnus; pedicel pale yellow with pink striations, puberulous, 1–1.3 cm long; perianth yellow, glabrous, puberulous along margins, 4.9–5.4 cm long, 8–10 mm wide at base, at anthesis curved 35–45°; free sepal strongly reflexed, fused sepals with apices not reflexed; staminode white, 6–8 by 3–4 mm, apex apiculate, base constricted; stamens with anthers connivent inside apex of corolla tube or slightly flared outside perianth apex; pollen *nutans* type, medium size ($51 \times 72 \mu\text{m}$), euoblate ($P/E = 0.71$), subisopolar ($DR/PR = 2.56$), with the distal hemisphere convex, spinulose, the proximal hemisphere planar to subconvex, psilate to granulose, the germination aperture distinctly protruding; ovary pale yellow, glabrous, 9–10 by 5–6 mm. Drupes glabrous, 1.6–1.9 by 1–1.3 cm.

SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: 8 mi from Quepos on road to Parrita, ca. sea level, *Kress et al.* 77-804 (DUKE); Finca 44 near Río Colorado beyond Villa Neily, elev. ca. 50 ft, *Kress & Cooper-Smith* 76-661 (DUKE), *Kress & Clarkson* 79-1095 (DUKE); near Coto 47 in herbaceous swamp, sea level, *Maas & McAlpin* 1465 (CR, U). **Panama.** DARIÉN: Alconorque swamp on Río Tuira ca. 3 mi NW of El Real, *Duke* 4817 (GH, US); .5 mi E of airstrip at El Real, *Lazor & Correa* 3398 (scz); Cerro Tacarcuna-Serranía, near Yaviza, elev. 50 m, *Gentry & Mori* 13506 (MO).

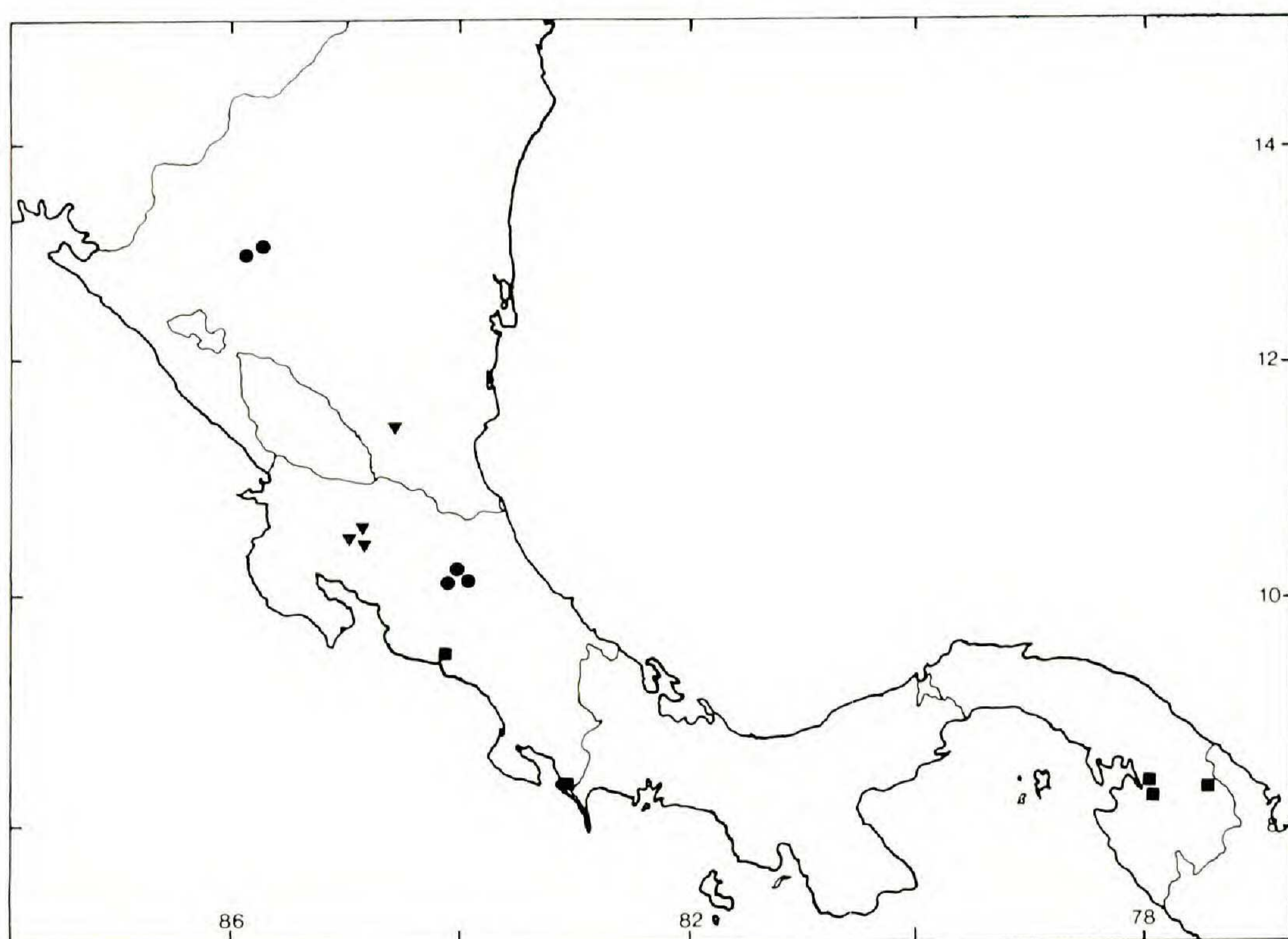
PHENOLOGY. Flowering and fruiting nearly all year, peaking July and August.

HABITAT AND DISTRIBUTION. This species is found on the Pacific Coastal Plain of Costa Rica and Panama, extending north to the Quepos area and south into Darién and South America, where it is more common (see MAP 3). It almost always occurs in dense stands in open swamps or standing water. *Heliconia marginata* is one of the few truly aquatic species of the genus.

RELATIONSHIPS. Among Central American species with pendent inflorescences, *Heliconia marginata* is most closely allied to members of the *nutans* group. However, differences in cincinnal bract morphology, floral structure, and pollen characteristics suggest that this species probably has closer relatives among South American taxa. The small inflorescences with red and yellow cincinnal bracts, the aquatic habitat, and the stiff, erect leaf blades readily distinguish *H. marginata* from other Central American heliconias.

7. ***Heliconia secunda*** R. R. Smith, *Phytologia* 30: 214. 1975. TYPE: Costa Rica, Heredia, along steep slope near road and waterfall, ca. 7 km N of Vara Blanca de Sarapiquí, elev. 5000 ft, *R. R. Smith* 2206 (holotype, FLAS; isotypes, A!, GH, MO, US).

Herb with *Musa*-like habit, 2–3 m tall. Leafy shoots solitary or in groups of 2 to 50; pseudostem glabrous, 0.6–2 m tall, 2.5–4 cm in diameter; leaves 2 to 5 per shoot; petiole green, glabrous, 40–120 cm long, 0.8–1.3 cm in diameter; blade with the base unequal, obtuse, the apex acute, the upper surface green, glabrous, with midrib green and glabrous, the lower surface light green to maroon, glabrous, with midrib green to yellow-green and maroon and glabrous to scurfy, the longest blade 80–120 by 20–40 cm. Inflorescence nodding to



MAP 3. Nicaragua, Costa Rica, and Panama, showing distribution of *Heliconia marginata* (squares), *H. secunda* vars. *secunda* (circles) and *viridiflora* (triangles).

pendent (sometimes contorted), to 50 cm long; peduncle red to yellow-red and green, glabrous to scurfy, 3.5–25 cm long, 1–1.3 cm in diameter; rachis flexuose and twisted or contorted, red, glabrous to scurfy, 9–11 mm in diameter at base; cincinnal bracts distichous or spirally arranged, 8 to 12 per inflorescence, oriented 90–120° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex acuminate, margins straight to revolute, inner surface red to orange and glabrous, outer surface red and glabrous to slightly scurfy, 10–14 cm long, 5.3–8 cm wide at base, $l/w = 1.8$. Floral bracts translucent, slowly decomposing after anthesis, pale yellow, glabrous to puberulous along midrib abaxially, 4–6 cm long, 1.5–2.3 cm wide at base. Flowers 10 to 25 per cincinnus; pedicel white to green to pale yellow, glabrous, 5–10 mm long; perianth yellow to green, glabrous except puberulous along sepal margins, 5–6 cm long, 7–10 mm wide at base, at anthesis curved 20–50°; free sepal reflexed, fused sepals with apices not reflexed; staminode white, apex 7–10 by 3–4 mm, tridentate with center tooth longer than blunt lateral lobes; stamens with anthers flared outside perianth apex; pollen *nutans* type, small ($43\text{--}44 \times 58\text{--}62 \mu\text{m}$), euoblate ($P/E = 0.70\text{--}0.74$), subisopolar ($DR/PR = 2.24\text{--}2.55$) with the distal hemisphere constricted, convex, spinulose, the proximal hemisphere planar to sub-convex, psilate to verrucose, the germination aperture distinctly protruding; ovary light green to yellow, glabrous, 6–9 by 5–6 mm. Drupes glabrous.

DISTRIBUTION. *Heliconia secunda* is found in middle-elevation forests of Costa Rica and Nicaragua (MAP 3).

VARIATION. This species consists of two varieties that differ primarily in flower color.

RELATIONSHIPS. *Heliconia secunda*, a member of the *nutans* group, is closely related to *H. nutans* (with pendent inflorescences) and *H. tortuosa* (with erect inflorescences). It is distinguished from other members of the group by its extremely twisted rachis, which gives the nodding to pendent inflorescences a very contorted appearance.

Key to the Varieties of *Heliconia secunda*

- Leaf blade with lower surface green; perianth yellow; ovary pale green. 7a. var. *secunda*.
 Leaf blade with lower surface usually maroon; perianth green; ovary yellow to green. 7b. var. *viridiflora*.

7a. *Heliconia secunda* var. *secunda*

PLATE III, C, D.

Leafy shoots in groups of 10 to 50; pseudostem 1.4–2 m tall, 2.5–4 cm in diameter; leaves 2 or 3 per shoot; petiole 50–100 cm long, 1–1.3 cm in diameter; longest blade 80–120 by 30–40 cm. Inflorescence nodding to pendent, to 50 cm long; peduncle red to yellow-red and green, scurfy, 8–25 cm long, 1–1.3 cm in diameter; rachis scurfy, 9–11 mm in diameter at base; cincinnal bracts spirally arranged, 9 to 12 per inflorescence, oriented 90–120° to axis of inflorescence, the middle bract with margins revolute, inner surface red becoming yellow at midrib, 10–12.5 cm long, 5.3–6 cm wide at base. Floral bracts 4–6 cm long, 1.5–2.3 cm wide at base. Flowers 15 to 25 per cincinnus; pedicel green, 5–10 mm long; perianth yellow, 5.5–6 cm long, 8–10 mm wide at base, at anthesis curved 20–30°; staminode 9–10 by 3 mm; ovary light green, 6–9 by 5–6 mm. Drupes 1.4 by 1 cm.

SPECIMENS EXAMINED. **Nicaragua.** JINOTEGA/MATAGALPA: in forest beside hwy. between Jinotega and Matagalpa, elev. 4000–4500 ft, *Bunting & Licht 981* (F, NY, US). JINOTEGA: region of Las Mercedes, sierra E of Jinotega, chiefly in dense wet mixed virgin forest (cloud forest), elev. 1200–1500 m, *Standley 10724* (F); Hwy. 3, 1.9 km NW of Aranjuez road entrance, elev. 1460–1480 m, *Stevens 9202* (MO). **Costa Rica.** HEREDIA: Catarata El Angel, Río La Paz Grande entre Cariblanco y Vara Blanca, elev. 1350 m, *Jiménez 2048* (F); at waterfall 3 mi from Cinchona, elev. 4100 ft, *Kress & Cooper-Smith 76-529* (DUKE), elev. 4400 ft, *Kress et al. 77-776* (DUKE); vic. of Vara Blanca, elev. 1750–1800 m, *Luteyn 3021* (DUKE); Cinchona, along road to Sarapiquí, near waterfalls, *Sheffy 68* (CR). SAN JOSÉ: Río Claro Valley, below La Palma, NE of San Jerónimo (Río La Hondura drainage), elev. 1000–1200 m, *Burger & Burger 7657A* (F), elev. 1500 m, *Burger & Stolze 5303* (F), *Burger & Visconti 10230* (F); Alto La Palma, elev. 4700 ft, *Kress et al. 77-773* (DUKE); along road between La Palma and La Hondura, *Sheffy 74* (CR); between Cascajal and San Isidro de Coronado, elev. 1600–1700 m, *Taylor 935* (DUKE).

PHENOLOGY. Flowering primarily March to August.

HABITAT AND DISTRIBUTION. *Heliconia secunda* var. *secunda* has been collected only around Jinotega in Nicaragua and in several localities in the Cordillera Central of Costa Rica (MAP 3). This variety inhabits old secondary growth in moist cloud forest at elevations of 1200–1500 m.

- 7b. ***Heliconia secunda* var. *viridiflora*** Daniels & Stiles, *Brenesia* **15**(Supl.): 42. 1979. TYPE: Costa Rica, Alajuela, ca. 2 km N of Bijagua, elev. 350 m, *Stiles s.n.*, 10 Sept. 1977 (holotype, USJ; isotypes, F!, US).

Heliconia viridiflora (Daniels & Stiles) Stiles, *Brenesia* **18**: 152. 1980.

Leafy shoots solitary or in groups of 2 to 4; pseudostem green, glabrous, 60–150 cm tall, 3–4 cm in diameter; leaves 5 per shoot; petiole 40–120 cm long, 8–10 mm in diameter; blade with base slightly attenuate to obtuse, lower surface green (becoming maroon at higher elevations), longest blade 90–120 by 20–30 cm. Inflorescence nodding or contorted, to 36 cm long; peduncle red, glabrous, 3.5–5 cm long, 1–1.2 cm in diameter; rachis flexuose and contorted, red, glabrous, 1 cm in diameter at base; cincinnal bracts distichous and often all arranged on same side of rachis, 8 to 10 per inflorescence, oriented 90° to axis of inflorescence, the middle bract with margins straight (sometimes overlapping near rachis), inner surface orange becoming red along margins, outer surface glabrous, 11–14 cm long, 7–8 cm wide at base. Floral bracts 4–4.5 cm long, 1.5–2 cm wide at base. Flowers 10 to 15 per cincinnus; pedicel pale yellow, 5–8 mm long; perianth white basally, green distally, 5–5.5 cm long, 7–9 mm wide at base, at anthesis curved 35–50°; staminode 7–10 by 3–4 mm; ovary light green to yellow, 8 by 5–6 mm wide. Fruits not seen.

SPECIMENS EXAMINED. **Nicaragua.** ZELAYA: ca. 6.3 km S of bridge at Colonia Yolaina and ca. 0.8 km S of ridge of Serranía de Yolaina on road to Colonia Manantiales (Colonia Somoza), elev. ca. 200–300 m, *Stevens 4881* (MO). **Costa Rica.** ALAJUELA: 3 km NNE of Bijagua along new road to Upala, elev. 450 m, *Burger & Baker 9815* (F), *9873* (F); wet forest 5 km S of Canalete near Río Zapate, along new road to Upala, elev. 100–200 m, *Burger & Baker 10009* (F). GUANACASTE: below Volcán Tenorio along road to Upala, elev. 800 ft, *Kress et al. 80-1216* (DUKE), elev. ca. 700 ft, *Kress et al. 80-1229* (DUKE). PUNTARENAS: San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. ca. 4000 ft, *Kress 78-1033* (DUKE).

PHENOLOGY. Flowering primarily August to November.

HABITAT AND DISTRIBUTION. *Heliconia secunda* var. *viridiflora* is found in the Cordillera de Yolaina of Nicaragua and the Cordillera de Guanacaste of Costa Rica between 200 and 500 m (MAP 3). This variety inhabits both primary and secondary forests.

RELATIONSHIPS. Variety *viridiflora* differs from the typical variety of *Heliconia secunda* in its flowers with green perianths, and its leaf blades with the lower surfaces varying from green with maroon borders to totally maroon. Because of the nonoverlapping flowering times of the two varieties, Stiles (1980) recognized this taxon as a species distinct from *H. secunda*. This phenological difference is not accepted here as sufficient evidence for elevating var. *viridiflora* to specific rank.

8. ***Heliconia nutans*** Woodson, *Ann. Missouri Bot. Gard.* **26**: 276. 1934. TYPE: Panama, Chiriquí, Volcán de Chiriquí, vic. of Casita Alta, *Woodson, Allen, & Seibert 968* (holotype, MO!; isotypes, GH!, MICH, NY!, US!).

FIGURE 10; PLATE III, E, F.

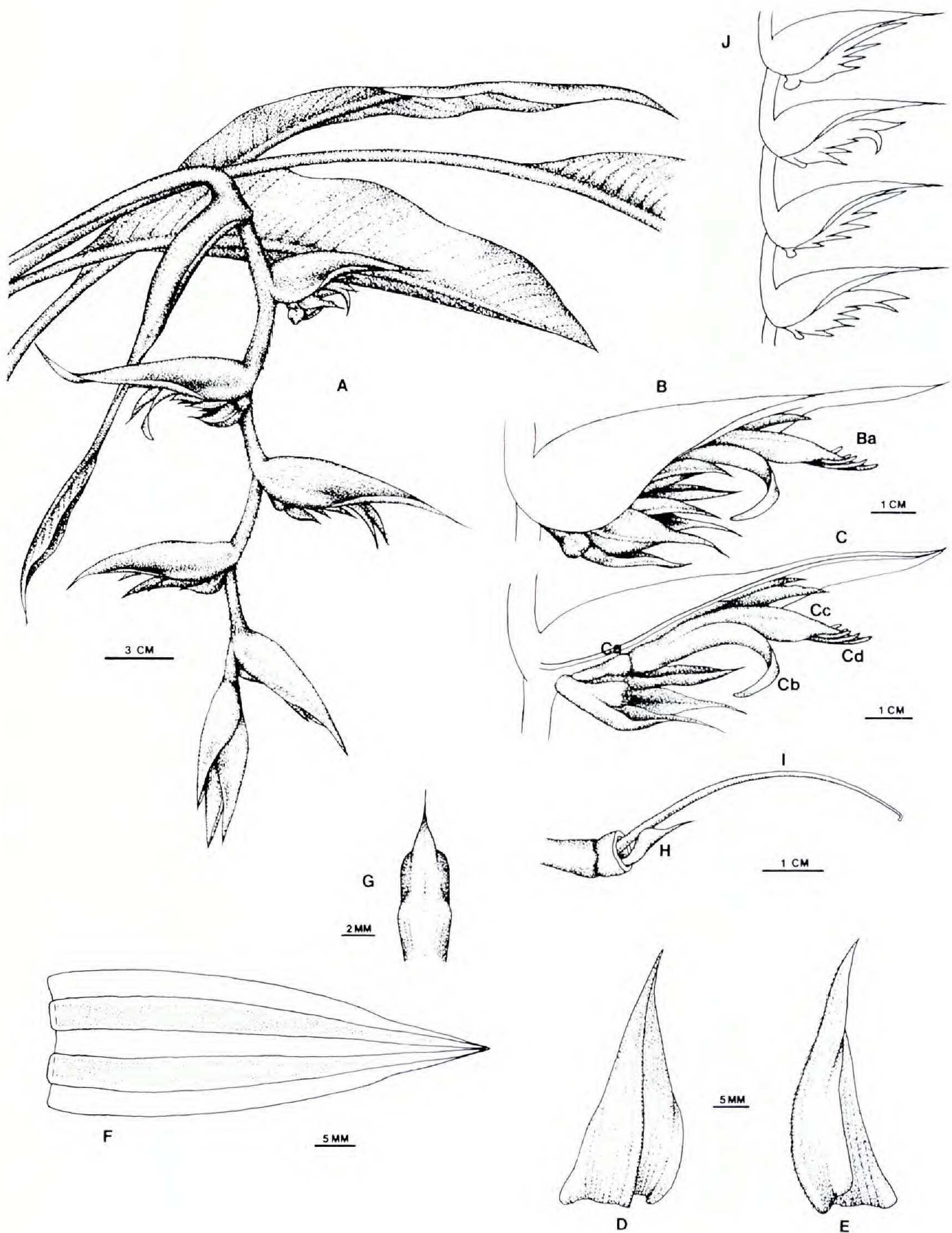


FIGURE 10. *Heliconia nutans*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, not reflexed; Cd, anthers, exserted). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma. J, inflorescence, schematic showing alternative orientation with all cincinnal bracts aligned on 1 side of inflorescence axis.

Heliconia allenii Standley & Williams, Ceiba 3: 189. 1953. TYPE: Panama, Chiriquí, Río Chiriquí Viejo, vic. Nueva Suiza, elev. 5000 ft, Allen 6255 (holotype, US!).

Heliconia villosa auct. non Klotzsch: Woodson & Schery, Ann. Missouri Bot. Gard. 32: 53. 1945, in part (Woodson and Schery included *H. irrasa*, *H. tortuosa*, and *H. nutans* in *H. villosa*).

Herb with *Musa*-like habit, 1–2.5 m tall. Leafy shoots in groups of 5 to 30; pseudostem light green and maroon, glabrous, 50–160 cm tall, 1.5–3.8 cm in diameter; leaves 3 to 5 per shoot; petiole green and maroon, glabrous, 20–68 cm long, 5–11 mm in diameter; blade with the base unequal, obtuse to truncate, the apex acute, the upper surface dark green, glabrous, with midrib green and glabrous, the lower surface green to maroon, glabrous, with midrib light green to maroon and glabrous to scurfy, the longest blade 50–105 by 15–31 cm. Inflorescence nodding to pendent (sometimes contorted), to 55 cm long; peduncle green and red to solid red; puberulous to tomentose with golden hairs, 5–50 cm long, 5–10 mm in diameter; rachis flexuose (sometimes twisted), red to orange-red (sometimes yellow), puberulous to tomentose with golden hairs, 5–10 mm in diameter at base; cincinnal bracts spirally arranged to distichous (sometimes all bracts aligned on 1 side of inflorescence axis), 5 to 13 per inflorescence, oriented 90–135° to axis of inflorescence, the basal bract often sterile, the middle bract with apex acute to acuminate, margins straight to revolute distally, inner surface red to red-orange and yellow and glabrous to puberulous, outer surface red to red-orange and glabrous to puberulous, 7–11 cm long, 4–7.5 cm wide at base, l/w = 1.6. Floral bracts translucent, persistent and papery when dried or decomposing after anthesis, pale yellow, glabrous to puberulous along midrib abaxially, 3.5–4.5 cm long, 1.3–2 cm wide at base. Flowers 10 to 20 per cincinnus; pedicel white to yellow, glabrous, 4–10 mm long; perianth yellow, glabrous to slightly puberulous, 4–5 cm long, 6–9 mm wide at base, at anthesis curved 30–50°; free sepal straight to reflexed, fused sepals with apices not reflexed; staminode white, apex 7–10 by 3–5 mm, trilobed with rounded lateral lobes; stamens with anthers flared outside perianth apex; pollen *nutans* type, small ($46 \times 54 \mu\text{m}$), suboblate ($P/E = 0.87$), subisopolar ($DR/PR = 2.49$) with the distal hemisphere constricted, convex, spinulose, the proximal hemisphere planar to subconvex, psilate to verrucose, the germination pore distinctly protruding; ovary light green, glabrous, 6–7 by 5–6 mm. Drupes glabrous, 1–1.1 by 1–1.1 cm.

SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: Las Alturas and vic., elev. 1600–1800 m, Maas & McAlpin 1486 (NY, U); San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. 4000 ft, Kress 76-570 (DUKE), 78-901 (DUKE), 78-1024 (DUKE). **Panama.** BOCAS DEL TORO: N slope of Cerro Pate Macho, elev. 1200–1400 m, Andersson & Sytsma 1311 (s). CHIRIQUÍ: no further locality, Wagner s.n., April 1858 (M); below Cerro Hornito, elev. 1000 m, Kress et al. 82-1368 (DUKE); Cerro Colorado, along road to copper mine beyond bridge over Río San Félix near town of San Félix, elev. 1390 m, Croat 37288 (MO); Cerro Colorado, near continental divide, elev. 1500 m, Antonio 1494 (DUKE, MO), 1531 (DUKE, MO), 1532 (MO), 4859 (DUKE, MO), 4861 (MO), 4863 (MO), 4912 (DUKE, MO); along road between Gualaca and Fortuna Dam site, 10.1 km NW of Los Planes de Hornito, elev. 1260 m, Antonio 4165 (MO); Gualaca–Fortuna Rd., elev. 1200–1400 m, Andersson 1306 (GB, s); NO de Campamento Fortuna (Hornito), sitio de regresando al SO del Campamento (Finca Pitti), elev. 1000–1200 m, Correa et al. s.n. (MO); La Fortuna

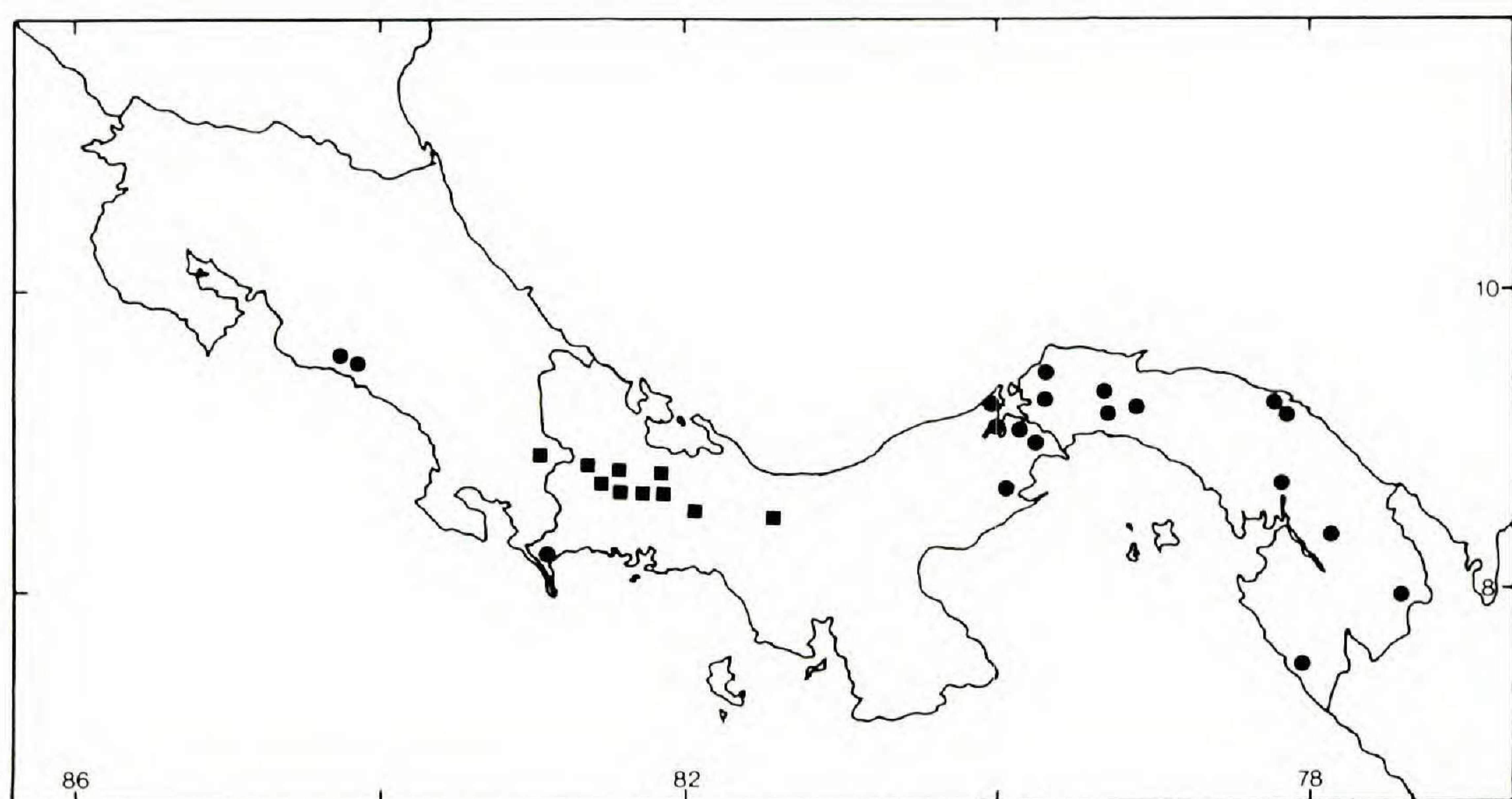
hydroelectric project, elev. ca. 1040 m, *Hammel 1990* (MO); La Fortuna Dam site, elev. 1100 m, *Kress & Hammel 83-1606* (DUKE); *Kress et al. 82-1344* (DUKE), *82-1345* (DUKE), *82-1355* (DUKE), *82-1356* (DUKE); area E of main camp at Fortuna Dam site, elev. 1400–1500 m, *Folsom et al. 5447* (MO); 2 km en el camino Cerro de la Muerte, elev. 6000 ft, *Correa 1244* (PMA); along road 1 km beyond Finca Alto Quiel toward Bajo Mono, elev. 5200 ft, *Luteyn 3716* (DUKE, MO); Cerro Horqueta, TTC-BMI Cloud Forest Litter Study, elev. ca. 1500 m, *Duke et al. 13678* (DUKE, MO, SCZ), *13667* (MO); SW slopes of Cerro Horqueta ca. 6 km NW of Boquete, elev. 1700–1800 m, *Wilbur et al. 15456* (DUKE); NW of Boquete, Cerro Horqueta, elev. 5000–5800 ft, *Dwyer et al. 438* (MO); Cerro Horqueta, elev. 1650 m, *Croat 26994* (MO); vic. of Boquete, lumber road into hills E of Río Caldera, elev. 4500–6500 ft, *Allen 4656* (GH); Boquete, Palo Alto, elev. 1300–1772 m, *Beliz 171* (PMA); Boquete, Finca Collins, *Blum & Dwyer 2583* (MO, SCZ); Monte Rey near Boquete, *Croat 15862* (MO); between Boquete and Monte Rey, *Croat & Porter 15653* (F, MO); E of Boquete on Cerro Azul near Quebrada Jaramillo, elev. 1500–1620 m, *Croat 26791* (MO); Boquete, elev. 3800 ft, *Davidson 668* (F, GH, US); Boquete, 5 mi from town near Finca Lerida, elev. 5300 ft, *Kress et al. 77-822* (DUKE); pastures around El Boquete, elev. 1000–1300 m, *Pittier 2936* (US); Bambito–Cerro Punta, elev. 2100 m, *Cochrane et al. 6294* (MO); Methodist Youth Camp between Nueva Suiza and Cerro Punta, *Croat 26271* (PMA); between Bambito and Cerro Punta, *Croat 10539* (F, MO, NY); Camino entre Bambito y La Amenaza, elev. 6000 ft, *Correa 1281* (PMA); roadside from Cerro Punta to Bambito, *Lazor & Correa 2730* (MO, SCZ); Bambito, elev. 1700 m, *Andersson 1300* (s); lower slope of Baru, E of Bajo Choro region, elev. 6000–6500 ft, *Hammel 3018* (MO); above hwy. along Río Chiriquí between Cerro Punta and Bambito, elev. 5200 ft, *Kress & Clarkson 79-1088* (DUKE); in forest along Río Chiriquí Viejo below Cerro Punta, elev. 5200 ft, *Kress & Clarkson 79-1089a* (DUKE), *79-1089b* (DUKE); Río Chiriquí Viejo, vic. of Nueva Suiza, elev. 5000 ft, *Allen 6255* (US); on road from Río Sereno to Volcán, *Antonio 1304* (MO); 2.2 mi E of El Hato del Volcán, *Luteyn 802* (DUKE); Cerro Pate Macho, elev. 1500–1700 m, *Andersson & Sytsma 1310* (GB, s); Río Chevo, elev. 1650 m, *Knapp 1451* (MO); Cerro Pelota, elev. 2300 m, *Knapp 1499* (MO). VERAGUAS: NE slopes of Cerro Delgadito just NW of Cerro Tute, S of town of Santa Fé, elev. 1000 m, *Luteyn 4039* (DUKE); Cerro Tute, elev. 800–1400 m, *Kress & Knapp 82-1410* (DUKE).

PHENOLOGY. Flowering principally February to August.

HABITAT AND DISTRIBUTION. This species is restricted to altitudes above 1000 m on the Pacific slopes of the western highlands of Panama and neighboring Costa Rica (MAP 4). *Heliconia nutans* inhabits disturbed primary and secondary forests often near streams or rivers. It is the only Central American *Heliconia* with a pendent inflorescence that occurs at elevations over 2000 m.

VARIATION. *Heliconia nutans* is composed of two morphologically distinct entities. One, which occurs primarily around Boquete and Cerro Punta in Chiriquí, Panama, has persistent, papery floral bracts, distichous cincinnal bracts, entirely green leaf blades, and a diminutive stature. The second entity is found in the mountains around La Fortuna and Cerro Colorado in eastern Chiriquí and has decomposing floral bracts, spirally arranged, somewhat contorted cincinnal bracts, maroon or green leaf-blade undersides, and a more robust stature. Their distribution is not entirely allopatric, and where the two entities overlap (e.g., above Gualaca) the first is found at lower elevations and in drier habitats than the second.

RELATIONSHIPS. *Heliconia nutans* is closely related to *H. secunda*, of Costa Rica



MAP 4. Costa Rica and Panama, showing distribution of *Heliconia nutans* (squares) and *H. platystachys* (circles).

and Nicaragua, with which it is often confused in the herbarium. The former species has a puberulous to tomentose rachis, a perianth 4–5 cm in length, and (in some cases) persistent floral bracts that appear papery when dried.

9. ***Heliconia platystachys*** Baker, Ann. Bot. (London) 7: 194. 1893 (excl. spec. cit. *Donnell-Smith 1873* (κ), which is *H. collinsiana* Griggs var. *velutina* Kress). TYPE: [Colombia,] Santa Marta, *Purdie s.n.* (lectotype, κ, chosen by Daniels, Kew Bull. 32: 682. 1978). PLATE IV, A, C.

Bihai platystachys (Baker) Griggs, Bull. Torrey Bot. Club 31: 445. 1904.

Heliconia catheta R. R. Smith, Phytologia 30: 65. 1975. TYPE: Panama, [Panamá,] near old Fort Lorenzo, mouth of Río Chagres, *Piper 6037* (holotype, US!).

Herb with *Musa*-like habit, 3–4 m tall. Leafy shoots in groups of 3 to 20; pseudostem green, glaucous, 1.3–2 m tall, 4–5 cm in diameter; leaves 3 to 6 per shoot; petiole green, glaucous, 90–100 cm long, 1–1.3 cm in diameter; blade with the base unequal, cordate, the apex acute, the upper surface dark green, glabrous, with midrib green and glabrous, the lower surface green, usually glaucous, with midrib light green and glaucous, the longest blade 1.3–1.7 m by 35–40 cm. Inflorescence pendent, to 80 cm long; peduncle red to green, puberulous to tomentose, 10–25 cm long, 1–1.6 cm in diameter; rachis flexuose, red becoming yellow near terminal cincinnal bracts, tomentose, 8–11 mm in diameter at base; cincinnal bracts spirally arranged, 10 to 20 per inflorescence, oriented 90–95° to axis of inflorescence, the basal bract sometimes sterile, the middle bract with apex acuminate, margins straight, inner surface puberulous and yellow-orange becoming green along margins, outer surface puberulous and red basally becoming yellow-green along margins and at apex, 11–16 cm long, 7.5–11 cm wide at base, l/w = 1.5. Floral bracts semitranslucent, decom-

posing after anthesis, yellow, glabrous to minutely puberulous abaxially, 3.5–4.5 cm long, 1–1.5 cm wide at base. Flowers 10 to 15 per cincinnus; pedicel pale yellow, puberulous, 1.5–2.5 cm long; perianth yellow to yellow-green, glabrous to minutely puberulous, 5.5–6 cm long, 1.1–1.3 cm wide at base, at anthesis curved 25–35°; free sepal reflexed, fused sepals with apices slightly reflexed; staminode white, 6–10 by 2–3 mm, apex apiculate; stamens with anthers flared outside perianth apex; pollen *nutans* type, large ($62 \times 76 \mu\text{m}$), suboblate ($P/E = 0.82$), subisopolar ($DR/PR = 2.65$), with the distal hemisphere constricted, convex, spinulose, the proximal hemisphere planar to subconvex, psilate to minutely spinulose, the germination aperture distinctly protruding; ovary pale yellow, puberulous to tomentose, 7–10 by 7–8 mm. Drupes sparsely puberulous, 1.7–1.8 by 1.4–1.5 cm.

SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: along hwy. 18 km N of Parrita, elev. ca. 25 m, *Kress & Cooper-Smith* 76-633 (DUKE); coastal road 11 mi from Parrita, ca. sea level, *Kress et al.* 77-803 (DUKE). **Panama.** CANAL ZONE: vic. of Nuevo Emperador, *Blum* 2394 (scz); near Fort Sherman Military Reservation, *Maas & Mori* 1754 (F, U); secondary tropical moist forest along road K-10, 4 km N of Arraiján, elev. 115 m, *Nee* 7160 (GH, PMA); near summit of Cerro Pelado, 1 km N of Gamboa, elev. 200–220 m, *Nee* 7439 (GH, MO, PMA); Río Agua Salud, near Frijoles, *Piper* 5856 (US); Barro Colorado Is., NE of Barrunga Pt. at edge of lake, *Croat* 5616 (MO), 5670 (scz); near #8 light house clearing, *Croat* 6387 (MO), *Dodge* 3486 (GH), *Fairchild* 17 (F), *Kenoyer* 232 (US); Summit Garden, *Croat* 10790 (F, NY); Albbrook Air Force Base Research Forest Site, *Stimson* 5068 (DUKE, PMA, scz); Albbrook, *Dwyer* 6599 (MO); along Pipeline Rd. near Gamboa, elev. ca. 75 m, *Kress & Cooper-Smith* 76-643 (DUKE), *Kress et al.* 77-860 (DUKE); Gaillard Hwy., *Kress* 83-1610 (DUKE); Las Cruces Trail, *Croat* 11875 (MO). CHIRIQUÍ: Puerto Armuelles, elev. 50 ft, *Davidson* 1179 (F); Península de Burica, vic. of San Bartolomé, elev. 0–50 m, *Woodson & Schery* 887 (BM), 891 (MO). COLÓN: 18 km past Sardinilla on way to Nombre de Dios, elev. 150–300 m, *Croat* 26113 (MO); N of Maria Chiquita on road to Portobelo, *Croat* 11353 (MO), *Knapp & Mallet* 5718 (MO); between Gatun Lock and Fort Sherman, ca. sea level, *Kress* 80-1243 (DUKE); along Hwy. 79, Quebrada Sardinilla, 6 km NE of Buena Vista, elev. 55 m, *Nee* 6571 (MO). DARIÉN: Punta Guayabo Grande, along beach, elev. 0–50 m, *Antonio & Hahn* 4217 (MO), *Knapp & Mallet* 3036 (MO); Santa Fé, elev. ca. 15 m, *Duke* 14269 (MO); vic. of Paya, Río Paya, *Stern et al.* 427 (GH, MO, UC, US); SW of Jaqué, *Sytsma & D'Arcy* 3483 (MO); vic. of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al.* 925 (GH, MO, UC, US). PANAMÁ: Vacamonte Pt., *Allen* 2959 (GH, MO); Cerro Campana, elev. 600 m, *Antonio* 1260 (MO); vic. of Río Tapia, *Bartlett & Lasser* 16623 (MO); TTC Albbrook Tower just outside Zone, *Blum* 1567 (scz); Río Canazas (afluente del Bayano) en el primer campamento, *Carrasquilla & Mendieta* 463 (DUKE, PMA); 5 mi from Interamerican Hwy. on road to Cerro Azul, *Croat* 11512 (scz); near old Fort Lorenzo, mouth of Río Chagres, *Piper* 6037 (US); Agricultural Exp. Station at Matias Hernández, *Pittier* 6813 (US); near big swamp E of Río Tocumén, *Standley* 26726 (US); 5 mi W of Chepo near Interamerican Hwy., *Tyson* 6701 (MO, PMA). SAN BLAS: Playón Chico, *Stier* 11 (MO), 130 (MO, US). PROVINCE UNKNOWN: *Kuntze s.n.*, Aug. 1874 (NY).

PHENOLOGY. Flowering primarily June to October.

HABITAT AND DISTRIBUTION. This species occurs in undisturbed forest and open secondary growth usually at elevations of less than 100 m, although several collections have been made at 600 m. *Heliconia platystachys* is distributed sporadically along the southern Pacific coast of Costa Rica and into Panama,

where it becomes more abundant in the provinces of Panamá, Colón, and Darién (MAP 4). It is also found in northern South America.

RELATIONSHIPS. In Central America, *Heliconia platystachys*, a member of the *nutans* group, is closely related to *H. collinsiana*, but it has closer relatives in South America. The puberulous cincinnal bracts and ovaries readily distinguish *H. platystachys* from other species of the *nutans* group.

NOMENCLATURE. The confusion over typification of *Heliconia platystachys* has been addressed by Daniels (1978). The problem arose when *H. platystachys* was redescribed by Smith (1975) as *H. catheta* from Panama. Smith made this decision after seeing only part of the type collection of *H. platystachys*. The type housed at Kew consisted of two separate entities: a Colombian collection made by Purdie and a Guatemalan one made by Donnell-Smith. The latter collection, the one seen by Smith, is attributable to *H. collinsiana*. Daniels, based on Baker's protologue, accurately chose the Purdie collection as the lectotype of *H. platystachys*, thereby reducing Smith's *H. catheta* to synonymy.

10. ***Heliconia collinsiana*** Griggs, Bull. Torrey Bot. Club **30**: 648. 1903. TYPE: Guatemala, Alta Verapaz, near Finca Sepacuité, *Cook & Griggs 352* (US!).

Bihai collinsiana (Griggs) Griggs, Bull. Torrey Bot. Club **31**: 445. 1904.

Heliconia rostrata auct. non Ruiz & Pavon: Standley & Steyer. Fieldiana Bot. **24**: 184. 1952.

Herb with *Musa*-like habit, 4–6 m tall. Leafy shoots in groups of 3 to 50; pseudostem glabrous to tomentose (sometimes glaucous), 1.2–3 m tall, 3.5–7 cm in diameter; leaves 3 to 5 per shoot; petiole green, glaucous, 40–120 cm long, 1.3–3 cm in diameter; blade with the base unequal, obtuse, the apex acute, the upper surface green to dark green, glabrous, with midrib green and glabrous, the lower surface green, glabrous or with white waxy coating, midrib light green, or maroon and glaucous, the longest blade 1.1–2.5 m by 28–70 cm. Inflorescence pendent, to 72 cm long; peduncle green to red, glabrous to velutinous with rusty hairs, 10–34 cm long, 1.1–1.9 cm in diameter; rachis flexuose, red (sometimes becoming yellow near apex), puberulous to velutinous, 6–13 mm in diameter at base; cincinnal bracts spirally arranged, 7 to 18 per inflorescence, oriented 90–100° to axis of inflorescence, the basal bract sometimes sterile, the middle bract with apex acuminate, margins straight to revolute, inner surface yellow-pink to red and glabrous, outer surface red to orange-red and glabrous to glaucous, 11–17 cm long, 6–8 cm wide at base, l/w = 2.0. Floral bracts opaque and decomposing after anthesis, white to pale yellow, glabrous to puberulous abaxially, 4.5–7 cm long, 1.5–2.5 cm wide at base. Flowers 10 to 20 per cincinnus; pedicel yellow to orange, glabrous to puberulous, 1–3 cm long; perianth yellow to orange, reddish along sepal margins, glabrous to puberulous, 4.6–6 cm long, 8–11 mm wide at base, at anthesis curved 15–25°; free sepal sometimes reflexed, fused sepals with apices not reflexed; staminode white, apex 1–1.7 cm by 3–6 mm, tridentate with center tooth longer than laterals; stamens with anthers flared outside perianth apex;

pollen *nutans* type, small to medium size ($52\text{--}60 \times 52\text{--}65 \mu\text{m}$), oblate-spheroidal ($P/E = 0.92\text{--}0.99$), subisopolar ($DR/PR = 2.67\text{--}3.28$), with the distal hemisphere convex, spinulose, the proximal hemisphere subconvex, psilate to verrucose, the germination aperture distinctly protruding; ovary yellow to pale green, glabrous, 6–10 by 6–10 mm. Drupes glabrous, 1.2–1.5 by 1.6–1.8 cm.

DISTRIBUTION. This species, found from Mexico to Nicaragua (MAP 5), is composed of two varieties that may overlap in geographic distribution but are separated by elevational differences.

RELATIONSHIPS. *Heliconia collinsiana* and *H. platystachys*, both members of the *nutans* group, are more closely related to each other than to any other Central American members of the genus. However, each of these taxa may be more closely related to some South American species than it is to the other. *Heliconia collinsiana* can be distinguished from *H. platystachys* by its pure red cincinnal bracts and its glabrous floral bracts and ovaries.

REMARKS. Several collections of a taxon that appears to be very closely related to *Heliconia collinsiana* var. *velutina* have been made in the states of Guerrero and Nayarit, Mexico. These plants differ from var. *velutina* in their much smaller stature (ca. 2 m) and their pubescent to tomentose calyxes. Smith (1968) named these individuals *H. \times mooreana*, believing them to be hybrids of *H. collinsiana* and *H. schiedeana*. Because of the rarity of natural hybrids in *Heliconia* (see section on hybrids) and the multiple collections of this taxon from several different localities in Mexico, Smith's interpretation is not accepted here. However, a decision as to the varietal status of this taxon must await further collections.

SPECIMENS EXAMINED. **Mexico.** GUERRERO: near km 339 on hwy. to Acapulco below Acahuizatlá, elev. 940 m, *Moore 6204* (GH); Acapulco and vic., *Palmer 311* (GH, K, US). NAYARIT: Arroyo de la Cosiscadora, elev. 60 m, *Ortega 49* (US).

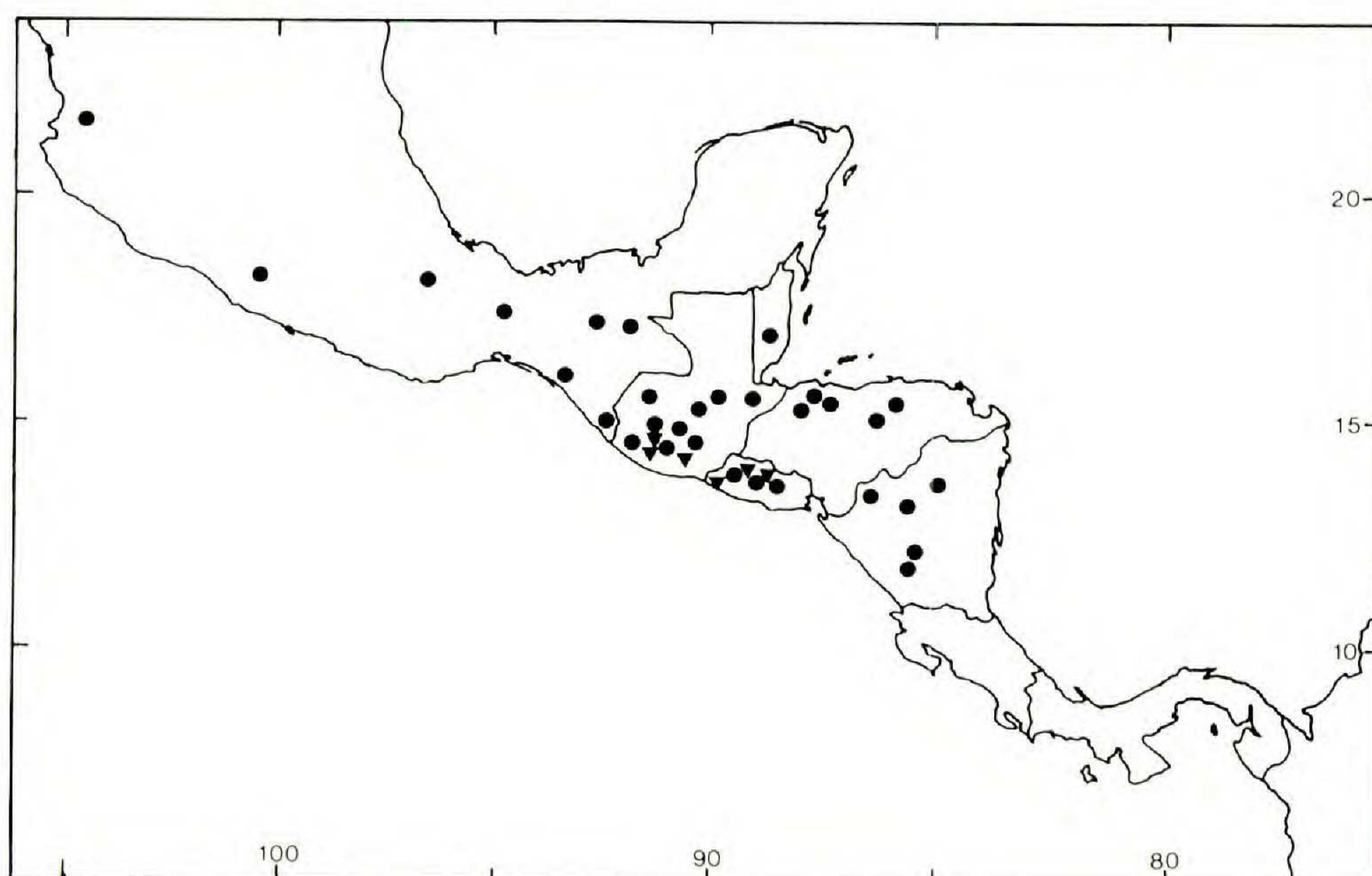
Key to the Varieties of *Heliconia collinsiana*

- Leaf blades with lower surface glaucous; peduncle and rachis glabrous to tomentose; perianth and ovary yellow. 10a. var. *collinsiana*.
 Leaf blades with lower surface not glaucous; peduncle and rachis tomentose to velutinous; perianth orange; ovary green. 10b. var. *velutina*.

10a. *Heliconia collinsiana* Griggs var. *collinsiana*

PLATE IV, B, D.

Herb to 4 m tall. Leafy shoots in groups of 5 to 50; pseudostem glaucous, 1.2–1.8 m tall, 3.5–5 cm in diameter; leaves with the petiole light green, 40–62 cm long, 1.3–1.5 cm in diameter, the blade having lower surface green with white waxy coating, the longest blade 1.1–1.5 m by 28–43 cm. Inflorescence with peduncle green to red, glabrous to tomentose, 10–34 cm long, 1.1–1.4 cm in diameter; rachis red, yellow near apical cincinnal bracts, puberulous to tomentose, 6–10 mm in diameter at base; cincinnal bracts 7 to 14 per inflorescence, the basal bract sometimes sterile, the middle bract with margins



MAP 5. Mexico and Central America, showing distribution of *Heliconia collinsiana* vars. *collinsiana* (circles) and *velutina* (triangles).

straight, inner surface yellow-pink to red, outer surface red to orange-red and often glaucous, 11–17 cm long, 6–8 cm wide at base. Floral bracts white to pale yellow, glabrous abaxially, 4.5–7 cm long, 1.5–2 cm wide at base. Flowers 10 to 12 per cincinnus; pedicel yellow to orange-yellow, glabrous to puberulous, 1.3–3 cm long; perianth yellow to orange-yellow, glabrous, 4.6–6 cm long, 8–11 mm wide at base, at anthesis curved 15–25°; staminode 1.1–1.7 cm by 3–6 mm wide; ovary yellow, 6–10 by 6–10 mm.

SPECIMENS EXAMINED. **Mexico.** CHIAPAS: NW side of Cerro Vernal, 25–30 km SE of Tonalá, elev. 400–600 m, *Breedlove* 25595 (DUKE, MO); 4 mi N of Tapachula along road to Nuevo Alemán, elev. 250 m, *Croat* 43790 (MO); 8.5 mi NE of Escuintla on gravel road to El Triunfo, elev. 250 m, *Croat* 43825 (MO); between Escuintla and Monte Ovando, 2.8 km NW of Turquiz, elev. 100 m, *Croat* 47469 (MO); Esperanza, Escuintla, *Matuda* 16693 (F), 18019 (F); Aguacorte Palenque, *Matuda* 3823 (GH); road to microwave tower about 1.7 mi from Hwy. 200, hwy. entrance 5.5 mi NW of Tres Picos, elev. 200 m, *Stevens et al.* 2412 (GH); Finca Prusia, municipio de Angel Albino Corzo, elev. 2400 ft, *Ton* 3591 (DUKE); N of Huixtla, elev. 500 m, *Taylor* 2644 (DUKE). MICHOACÁN/GUERRERO: Sierra Madre, elev. 5–800 m, *Anonymous s.n.*, Jan. 1899 (GH, US). NAYARIT: 8–10 mi W of Tepic along road over mtn. to Jalcocotan, elev. 4000 ft, *Gentry & Gilly* 10847 (DUKE). OAXACA: Distr. of Tuxtepec, Chiltepec and vic., elev. 20 m, *Martínez-Calderón* 99 (GH, US); ravine 35 km E of Mathias Romero, 4 km W of Palomares on trans-isthmus highway, *Moore* 8111 (A). VERACRUZ: Fortín de las Flores (posada Loma), elev. 850 m, cultivado, *Nevling & Gómez-Pompa* 312 (GH). **Guatemala.** ALTA VERAPAZ: 22 mi from Tactic near Tucunu, on road to El Estor, elev. 700 ft, *Kress et al.* 77-747 (DUKE); vic. of Secanquim, elev. 550 m, *Maxon & Hay* 3187 (US); near Pancajche, elev. 360 m, *Standley* 70639 (F); Cubilquitz, elev. 350 m, *Von Tuerckheim* 8468 (GH, K, NY, US). CHIMALTENANGO: *Johnston* 993 (F). CHIQUIMULA: Río Grande (Río Concepción), on Socorro Mtn., above Finca San José, SE of Concepción de las Minas, elev. 1200–1700 m, *Steyermark* 31128 (F). ESQUINTLA: between Rodeo and Osuna, below Volcán de Fuego, elev. 2300 ft, *Kress et al.* 77-753 (DUKE); La Trinidad on road between Escuintla and Finca

Zapote, elev. 780 m, *Standley 65042* (F); Masagua, elev. 400 m, *J. D. Smith s.n.*, April 1890 (US). HUEHUETENANGO: between Ixcán and Río Ixcán, Sierra de los Cuchumatanes, elev. 150–200 m, *Steyermark 49342* (F). IZABAL: 10–15 km W of El Estor, thickets along road in flat terrain on red clay, *Harmon & Dwyer 4359* (MO, US); vic. of Quirigua, elev. 75–225 m, *Standley 24480* (GH, US). QUEZALTENANGO: El Palmar, elev. 2300 ft, *Kellerman 6078* (F); Palmar, elev. 2300 ft, *Kellerman s.n.*, Feb. 1906 (US). RETALHULEU: Río Talcúlan W of Retalhuleu, elev. 300 m, *Standley 87338* (F). SAN MARCOS: Río Mopa, below Rodeo, elev. 600 m, *Standley 68796* (F). SANTA ROSA: near El Molino, elev. 600 m, *Standley 78520* (F); region of Platanares, between Taxisco and Guazacapan, elev. 220 m, *Standley 79130* (F). SUCHITEPEQUEZ: Río Sis, elev. 1300 ft, *Donnell-Smith 2804* (K, US); along Río Madre Vieja, above Patulul, elev. 450 m, *Standley 62244* (F); E slopes of Volcán Santa Clara, above Chicacao, elev. 1250 m, *Steyermark 46777* (F); vic. of Tiquisate, elev. 100 m, *Steyermark 47633* (F). **Belize.** STANN CREEK: Middlesex, elev. 200 ft, *Schipp 375* (BM, F, GH, K, MO, NY, UC); Stann Creek R.R., *Gentle 2106* (NY). **El Salvador.** AHUACHAPÁN: along road to Tacuba, 2–3 mi NW of San Francisco Menéndez, elev. 500 m, *Croat 42091* (MO). LA LIBERTAD: Colina de Santa Tecla, *Calderón 1851* (US); Finca Santa María, W of Santa Tecla, elev. 750 m, *Carlson 162* (F), elev. 800 m, *Inst. Trop. Inv. Cient. (ITIC) 1206* (MO). SANTA ANA: elev. 700 m, *ITIC 1201* (MO). SAN SALVADOR: elev. 670 m, *ITIC 1204* (MO); vic. of San Salvador in thicket along stream, elev. 650–850 m, *Standley 20551* (US). SAN VICENTE: vic. of San Vicente, elev. 350–500 m, *Standley 21751* (GH, NY, US). SONSONATE: Finca Chilata, stream bank, *Standley 19330* (GH, NY, US). **Honduras.** ATLÁNTIDA: vic. of San Alejo near Río San Alejo, *Standley 7715* (F); rain forest on slopes, Lancetilla Valley ca. 3 mi S of Tela, elev. 200–500 ft, *Webster et al. 12642* (F, MO); Lancetilla Valley, near Tela, *Pfeifer 2126* (US); E of La Ceiba, in rocky ravine, slopes near Puerte Alto on S.F. Co. R.R., elev. 800 ft, *Yuncker et al. 8537* (F, GH, MO, NY, S, UC, US). COLÓN: Trujillo, Río Negro, *Saunders 556* (NY), *703* (NY). CORTES: Mt. Bella Vista above San Pedro Sula, *Barkley & Leiva s.n.*, 4 Oct. 1969 (GH). OLANCHO: Orillas del Patuca, cerca Río Guayape, *G. Cruz s.n.*, 2 March 1973 (MO); rich soil of montane forest between Cofradia and Rancho Quemado, *Barkley & Errazuri 40307* (MO). **Nicaragua.** GRANADA: Comarca La Fuente, elev. 600 m, *Castro & Montiel 609* (DUKE, MO); Volcán Mombacho, elev. 350–500 m, *Moreno 413* (MO), *439* (MO), *1466* (MO). JINOTEGA: NE de Wiwilí, entre El Carmen y Wamblan, elev. 250–400 m, *Araquistain & Castro 1859* (DUKE), *Araquistain & Moreno 1508* (DUKE). MANAGUA: 2 mi from El Crucero on the Pan Am Hwy., elev. 2700 ft, *Kress et al. 77-758* (DUKE); between El Crucero and house of Finca Santa Julia, elev. 600–900 m, *Standley 8380* (F); along Hwy. 8 ca. 2.4 km SW of intersection with Hwy. 2, km 28, elev. ca. 700 m, *Stevens 3982* (DUKE), *5167* (DUKE). NUEVA SEGOVIA: Jalapa, *Atwood et al. 6773* (MO). ZELAYA: tall forest about Yauya, 18 km SE of La Luz, elev. 150–200 m, *Bunting & Licht 581* (F, NY).

PHENOLOGY. Flowering mainly January to August (dry season and early part of rainy season); some mature inflorescences all year.

HABITAT AND DISTRIBUTION. Variety *collinsiana* inhabits open secondary growth and well-drained soils at middle to higher elevations (up to 1200 m) from southern Mexico to central Nicaragua (MAP 5). It is the northernmost species of *Heliconia* with a pendent inflorescence and is almost completely allopatric with all other species having the same inflorescence type.

- 10b. ***Heliconia collinsiana*** Griggs var. ***velutina*** Kress, J. Arnold Arbor. **69**: 255. 1981. TYPE: Guatemala, Quezaltenango, lower slopes of Volcán Santa María de Jesús, along hwy. to Quezaltenango near Santa María de Jesús, elev. 1450 m, *Kress, Clarkson, & McDade 77-756* (holotype, DUKE; isotypes, F, K).

Herb to 6 m tall. Leafy shoots in groups of 3 to 8; pseudostem glabrous to tomentose, 2.5–3 m tall, 7 cm in diameter; leaves with the petiole green, 1–1.2 m long, 2.5–3 cm in diameter, the blade with lower surface green and glabrous, the longest blade 2.2–2.5 m by 65–70 cm. Inflorescence with peduncle rusty red, velutinous to villous with rusty hairs, 16–30 cm long, 1.5–1.9 cm in diameter; rachis red, tomentose to velutinous, 1.1–1.3 cm in diameter at base; cincinnal bracts 15 to 18 per inflorescence, the basal bract usually fertile, the middle bract with margins revolute, inner surface red, outer surface deep red and glabrous, 14–17 cm long, 6–7.5 cm wide at base. Floral bracts white, glabrous to puberulous abaxially, 5–6 cm long, 1.5–2.5 cm wide at base. Flowers 15 to 20 per cincinnus; pedicel pale orange, puberulous, 1–1.7 cm long; perianth pale orange, glabrous to puberulous, 5.5–5.7 cm long, 8–9 mm wide at base, at anthesis curved 15–20°; staminode 9–12 by 4–5 mm; ovary pale green, 7–8 by 7–9 mm.

SPECIMENS EXAMINED. **Guatemala.** ESCUINTLA: Finca Monterrey, S slope of Volcán de Fuego, elev. 1140–1260 m, *Standley 64533* (F). GUATEMALA: without further locality, elev. 5000 ft, *Donnell-Smith 1873* (K). QUEZALTENANGO: road to Finca Pireneos near Santa María de Jesús, elev. 4000 ft, *Kress et al. 76-663* (DUKE); Volcán Santa María, elev. 4500 ft, *Kellerman 6073* (F), 6076 (US); Finca Pireneos below Santa María de Jesús, elev. 1350–1380 m, *Standley 68427* (F); between Finca Pireneos and Finca Soledad, lower S-facing slopes of Volcán Santa María between Santa María de Jesús and Calahuache, elev. 1300–1400 m, *Steyermark 33575* (F). SANTA ROSA: Cenaguilla, elev. 4000 ft, *Heyde & Lux 4635* (GH, K, US). SUCHITEPEQUEZ: Finca Mocá, in bushy growth at edge of barranca, elev. 5000 ft, *Skutch 2101* (GH). **El Salvador.** AHUACHAPÁN: Sierra de Apaneca in region of Finca Colima, *Standley 20081* (US). SANTA ANA: moist canyon slope, W side of Cerro del Aguila, elev. 1650 m, *Tucker 1291* (F, K, UC, US). SONSONATE: Cerro los Naranjos, *ITIC 1207* (MO).

PHENOLOGY. Flowering and fruiting mainly during dry season (January to April) and early part of rainy period (May to July); some inflorescences produced all year.

HABITAT AND DISTRIBUTION. *Heliconia collinsiana* var. *velutina* is found on steep forested slopes at middle to higher elevations (> 1300 m) in the Guatemalan and Salvadorian highlands (MAP 5). It is one of the few Central American heliconias found at such high elevations.

RELATIONSHIPS. This variety is distinguished from var. *collinsiana* by its greater stature, its lack of glaucous lower leaf surfaces, its hairy peduncle and rachis, its orange flowers, and its growth at higher altitudes (above 1300 m).

11. ***Heliconia curtispatha*** Petersen in Martius & Eichler, Fl. Brasil. 3: 15. 1890.
TYPE: Panama, [Canal Zone,] prope Gatún, M. Jan. Flor., *M. Wagner s.n.*, Jan. 1858 (holotype, M!). PLATE V, A, C.

Bihaia curtispatha (Petersen) Kuntze, Rev. Gen. Pl. 2: 685. 1891.

Bihai longa Griggs, Bull. Torrey Bot. Club 31: 446. 1904; *Heliconia longa* (Griggs) Winkler in Engler & Prantl, Nat. Pflanzenfam. ed. 2. 15a: 536. 1930. TYPE: Costa Rica, Alajuela, El Pez road from Buena Vista to San Carlos Valley, *Cook & Collins 47* (holotype, US!).

Heliconia rostrata auct. non Ruiz & Pavon: Woodson & Schery, Ann. Missouri Bot.

Gard. 32: 54. 1945, in part (Woodson & Schery included *H. curtispatha* and a hybrid in *H. rostrata*).

Herb with *Musa*-like habit, 6–7 m tall. Leafy shoots in groups of 5 to 25; pseudostem green, glabrous, 1.8–3 m tall, 5–6.5 cm in diameter; leaves 4 to 7 per shoot; petiole green to reddish green, glabrous, 90–145 cm long, 1.5–2.3 cm in diameter; blade with the base unequal, cordate, the apex acute, the upper surface dark green, glabrous, with midrib light green to green and glabrous, the lower surface green, covered with white waxy coating, with midrib yellow to red-green and glabrous, the longest blade 1.9–2.3 m by 35–55 cm. Inflorescence pendent, to 1.6 m long; peduncle red (sometimes yellow), glabrous to scurfy, 28–37 cm long, 1.3–1.8 cm in diameter; rachis flexuose, red to red-orange, puberulous to scurfy, 1.2–1.8 cm in diameter at base; cincinnal bracts distichous to spirally arranged, 20 to 40 per inflorescence, oriented 130–145° to axis of inflorescence, the basal bract usually sterile, the middle bract with apex acute to acuminate, margins straight to involute, inner surface yellow-orange to pink and puberulous to tomentose with rusty hairs, outer surface red to yellow-orange near rachis and puberulous, 8.5–11.5 cm long, 6.5–9 cm wide at base, $l/w = 1.3$. Floral bracts opaque, persistent, white to yellow, tomentose to velutinous abaxially, 5.5–6.5 cm long, 1.6–2.3 cm wide at base. Flowers 10 to 20 per cincinnus; pedicel white to pale yellow, glabrous to puberulous, 1.1–2 cm long; perianth white to yellow and glabrous basally, deep yellow and slightly puberulous toward apex, 5.5–6.5 cm long, 9–10 mm wide at base, at anthesis curved 70–90° and parabolic; free sepal somewhat reflexed, fused sepals with apices reflexed; staminode white, 6–8 by 2–3 mm, apex cuspidate; stamens with anthers connivent inside apex of corolla tube; pollen *curtispatha* type, medium size ($57 \times 71 \mu\text{m}$), suboblate ($P/E = 0.82$), isopolar ($DR/PR = 0.99$), with the distal hemisphere subconvex, spinulose, the proximal hemisphere convex, minutely spinulose, the germination pore distinct and somewhat sunken; ovary white, glabrous, 7–11 by 5–7 mm. Drupes glabrous, 1.7 by 1 cm.

SPECIMENS EXAMINED. **Nicaragua.** ZELAYA: 5 mi W of Bonanza, *Atwood & Neill 6995* (MO); 20 mi W of Rama near Río Micito, elev. 200 ft, *Kress et al. 77-759* (DUKE); vic. of El Recreo, on Río Mico, elev. ca. 30 m, *Standley 19407* (F). **Costa Rica.** ALAJUELA: 5 km S of Canalete near Río Zapate and along new road to Upala, elev. 100–200 m, *Burger & Baker 10000* (F); upper Río Sarapiquí near Cariblanco and along road to Colonia Virgen del Socorro, elev. 800 m, *Burger & Antonio 11133* (F); steep bank above Quebrada Arrayanes, Cariblanco, elev. 900 m, *Lent 3536* (F); 8 km NE of Villa Quesada, near Artezalea and Methodist Rural Center, elev. 550 m, *Molina et al. 17219* (F, NY); forests along Río San Rafael, near hot springs, Hacienda La Marina, ca. 14 km NE of Villa Quesada, elev. 50 m, *Molina et al. 17422* (F, NY); near Santa Clara, elev. 2100 ft, *Kress et al. 77-768* (DUKE); near San Miguel, elev. 1700 ft, *Kress & Cooper-Smith 76-531* (DUKE); near San Miguel, *Sheffy 69* (CR). CARTAGO: near Turrialba, 2 km W of Oriente along Río Vueltas, *Sheffy & Tosi 58* (CR). HEREDIA: Finca La Selva, new property, *Hammel 11459* (DUKE). LIMÓN: between Siquirres and Río Pacuare, and hills S of RR bridge over Río Pacuare, elev. 50–100 m, *Burger & Liesner 7000* (F); in old banana plantation 1 km W of Moín, elev. 25 m, *Kress et al. 76-617* (DUKE); 5 mi from Puerto Limón on road to Siquirres, elev. ca. 100 ft, *Kress et al. 77-789* (DUKE); Cimarrones, ca. 10 km E of Siquirres, elev. 200 m, *Maas 1133* (F, U). PUNTARENAS: San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. 4000 ft, *Kress 76-577* (DUKE), *78-1023* (DUKE). SAN JOSÉ: bords du río de las Vueltas, Tucurrique, elev. 635 m, *Tónduz 12923*

(K, M, US, W). PROVINCE UNKNOWN: forêts de Tsallo, elev. 200 m, *Tónduz* 9433 (US, W); lieux humides à Zent, elev. 31 m, *Tónduz* 14542 (F (photo), NY). **Panama.** CANAL ZONE: Paraiso, *Dwyer* 7154 (MO). COCLÉ: between La Junta and Limón, elev. 800–1000 m, 5 hr walk N of Alto Calvario, *Folsom* 5882 (MO); above La Pintada on road to Coclecito, elev. 1600–1700 ft, *Kress et al.* 80-1165 (DUKE); La Pintada–Cascajal, elev. 700–800 m, *Andersson & Sytsma* 1255 (MO, S). COLÓN: forest on hills above road 18 km past Sardinilla on way to Nombre de Dios, elev. 150–300 m, *Croat* 26093 (MO); Cerro Santa Rita, elev. 800–900 ft, *Antonio* 1787 (MO); Santa Rita Ridge, *Dwyer & Gentry* 9549 (F, MO), *Sytsma* 1583 (MO); between France Field, Canal Zone, and Cartival, *Standley* 30425 (US); along Río Guanche, elev. 40 m, *Antonio* 1217 (MO); Río Guanche, elev. 50 ft, *Kress & Hammel* 80-1157 (DUKE); Portobelo, Río Buenaventura, at first bridge leaving on road from Portobelo, *Kennedy* 468 (PMA); SW of Cerro Bruja, elev. 600–700 m, *Andersson & Sytsma* 1241 (G, MO, S). DARIÉN: Punta Guayabo Grande to Río Jaqué, elev. 5–200 m, *Antonio & Hahn* 4384 (MO); Enseñada del Guayabo, *Garwood* 1200 (MO); between Quebrada Venado and Peje Swamp on headwaters of Río Tuqueza, *Bristan* 1041 (MO); E slope of Cerro Sapo, elev. 2500 ft, *Hammel* 1319 (MO); Cerro Pirre, *Bristan* 517 (NY). PANAMÁ: 3 mi above Goofy Lake near Cerro Azul, *Croat* 11571 (F, MO, NY); Cerro Jefe, *D'Arcy et al.* 1957 (F, MO), elev. 2300 ft, *Kress et al.* 77-864 (DUKE); Alto de Pacora, below Cerro Jefe, elev. 800–900 m, *Kress et al.* 76-635 (DUKE), *Kress & Hammel* 83-1573 (DUKE); Campo Tres, 3 mi NE of Alto de Pacora, elev. 500–800 m, *Liesner* 537 (MO); road to Cartí, *Antonio* 1288 (MO); El Llano–Cartí Rd., elev. 100–200 m, *Andersson & Sytsma* 1259 (GB, MO, S), elev. 300–400 m, *Folsom* 2561 (MO), *Folsom et al.* 6190 (MO), *Kress & Hammel* 82-1333 (DUKE); 6 km above Pan Am Hwy. on road from El Llano to Cartí–Tupile, elev. ca. 200 m, *Kennedy* 1774 (F, MO, NY); 2.4 mi N of Interamerican Hwy. toward El Llano and Cartí, elev. ca. 1700 ft, *Luteyn* 4126 (DUKE); El Llano–Cartí Rd., 5 km N of Pan Am Hwy. at El Llano, elev. ca. 300 m, *Nee* 7928 (MO, SCZ), premontane wet forest, *Nee* 7944 (MO, US). SAN BLAS: hills SW of Puerto Obaldía, *Croat* 16721 (MO).

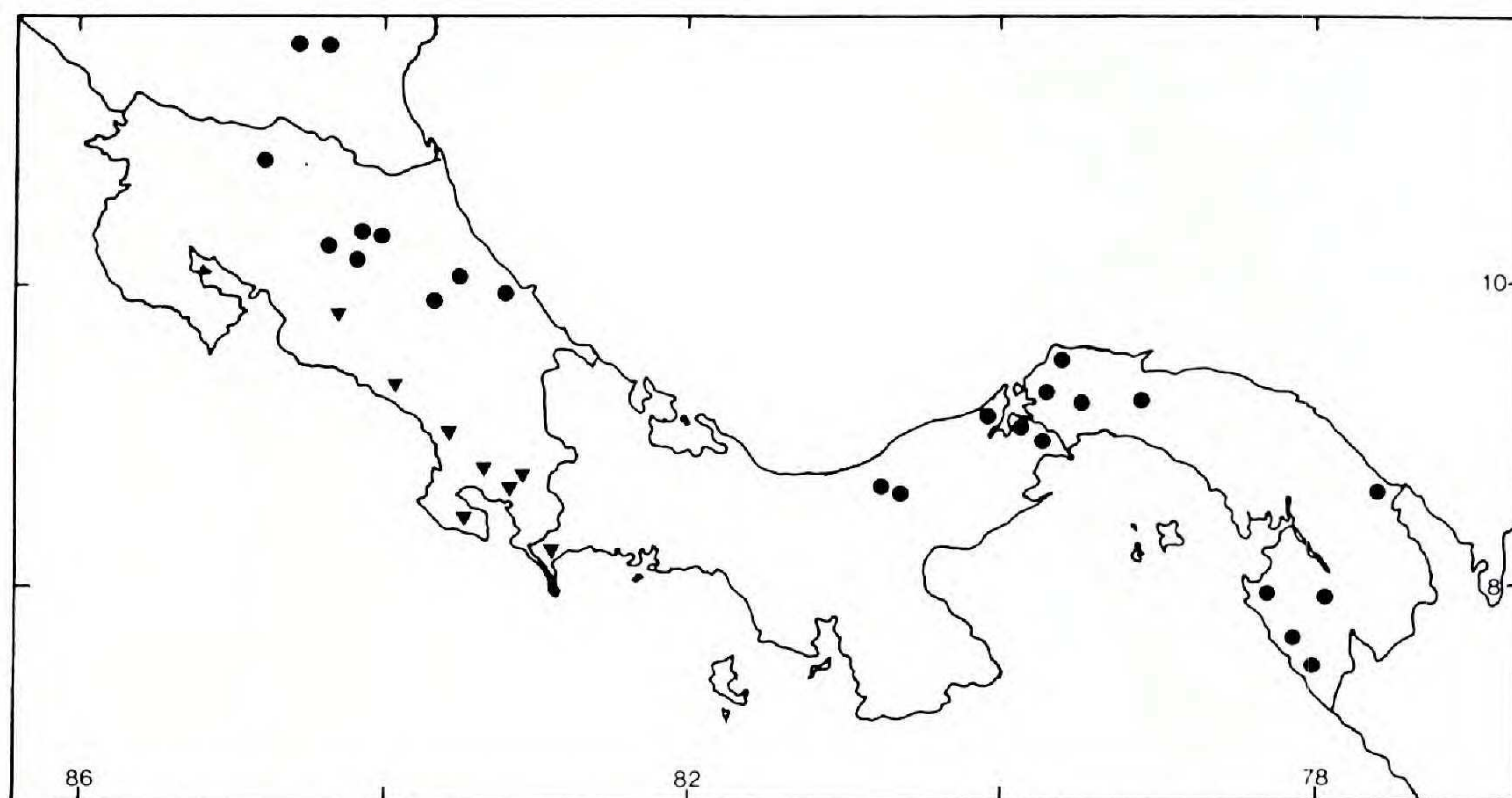
PHENOLOGY. Flowering throughout year, with slight peak during early rainy season (June to September).

HABITAT AND DISTRIBUTION. At higher elevations (above 100 m), *Heliconia curtispatha* inhabits old secondary growth and undisturbed forested slopes. At lower elevations, especially around the Limón area in Costa Rica, this species will invade old banana plantations and other disturbed areas. *Heliconia curtispatha* is distributed from southern Nicaragua to eastern Panama and Colombia. It is primarily found on the Caribbean side of the central cordilleras of Costa Rica and Panama from sea level to 900 m (MAP 6).

VARIATION. *Heliconia curtispatha* is generally morphologically homogeneous except for a distinct color form that is found in the Caribbean lowlands around Limón in Costa Rica. Plants found in this area have distinctive orange to yellow rachises, as opposed to the normal red ones common throughout the range.

RELATIONSHIPS. This species shares a unique common ancestor with *Heliconia stilesii*; together these species constitute the monophyletic *curtispatha* group. This group is allied to the *pogonantha* group but differs in its leaf blades with glaucous lower surfaces and its glabrous, parabolic perianths, as well as in several pollen characters.

NOMENCLATURE. Daniels and Stiles (1979) mistakenly applied Griggs's synonym *Heliconia longa* to this taxon.



MAP 6. Southern Nicaragua, Costa Rica, and Panama, showing allopatric distribution of *Heliconia curtispatha* (circles) and *H. stilesii* (triangles).

12. ***Heliconia stilesii*** Kress, Brenesia **19/20**: 202. 1982. TYPE: Costa Rica, Puntarenas, slopes above airport at Golfito, elev. 50 ft, *Kress & Clarkson* 79-1096 (holotype, DUKE!; isotypes, CR!, F!).

FIGURE 11; PLATE V, B, D.

Heliconia curtispatha auct. non Petersen: Griggs, Bull. Torrey Bot. Club **42**: 316. 1915; Daniels & Stiles, Brenesia **15**(Supl.): 19. 1979.

Heliconia platystachys auct. non Baker: Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18**: 184. 1937.

Herb with *Musa*-like habit, 5–6 m tall. Leafy shoots in groups of 7 to 16; pseudostem pale yellow-green, glabrous to slightly glaucous, 2.4–3.5 m tall, 6–7 cm in diameter; leaves 4 to 6 per shoot; petiole yellow-green, glabrous, 1.2–1.9 m long, 1.5–2.3 cm in diameter; blade with the base unequal, truncate to cordate, the apex acute, the upper surface dark green, glabrous, midrib light green and glabrous, the lower surface light green, covered with white waxy coating, midrib yellow-green with maroon and glabrous, the longest blade 1.7–2.3 m by 45–55 cm. Inflorescence pendent, to 1 m long; peduncle red, glabrous to scurfy, 10–75 cm long, 1.1–1.8 cm in diameter; rachis strongly flexuose with cincinnal bracts often touching each other, red, scurfy, 1–1.4 cm in diameter at base; cincinnal bracts distichous, 20 to 35 per inflorescence, oriented 135–155° to axis of inflorescence, the basal bract often sterile, the middle bract with apex acute to acuminate, margins straight to overlapping near rachis, inner surface pink to white and pubescent to tomentose with rusty hairs, outer surface rose-red and puberulous to scurfy, 8.5–9 cm long, 6–7.5 cm wide at base, l/w = 1.3. Floral bracts opaque, persistent, pale yellow (sometimes pink), tomentose to velutinous abaxially, 4.5–6.5 cm long, 1.4–1.8 cm wide at base. Flowers 10 to 20 per cincinnus; pedicel white to yellow, glabrous, 1.5–1.9 cm long; perianth white to pale yellow basally, deep yellow toward apex, glabrous, puberulous

along margins, 5.1–6.2 cm long, 1 cm wide at base, at anthesis curved 55–80° and parabolic; free sepal straight to slightly reflexed, fused sepals with apices slightly reflexed; staminode white, 5–8 by 3–4 mm, apex cuspidate; stamens with anthers connivent inside apex of corolla tube; pollen *curtispatha* type, medium size ($53 \times 66 \mu\text{m}$), suboblate ($P/E = 0.82$), isopolar ($DR/PR = 1.17$), with the distal hemisphere convex to subconvex, spinulose, the proximal hemisphere convex, minutely spinulose, the germination aperture distinct and somewhat sunken; ovary white, glabrous, 8–9 by 5–6 mm. Drupes glabrous, 1.2–1.5 cm by 7–9 mm.

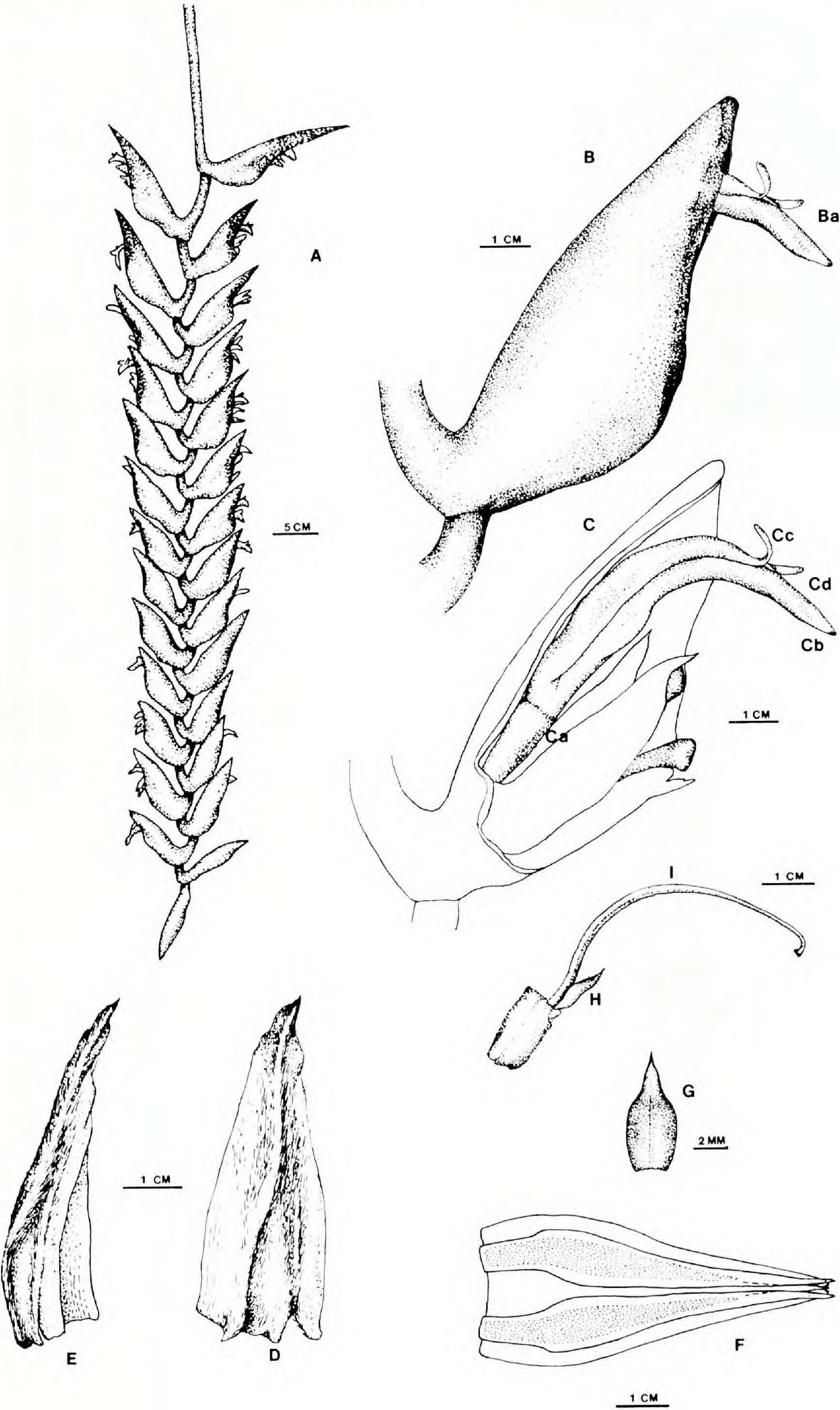
SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: 5 km W of Palmar Norte on road to Puerto Cortes, elev. 300 m, *Lent 158* (CR, F); Esquinas Forest, elev. 30 m, *Allen 6289* (GH); entre Los Ríos Piedras Blancas y Esquinas, Osa, elev. 75 m, *Jiménez 2249* (F, NY); Esquinas Forest Reserve near Río Claro, elev. ca. 100 ft, *Kress 78-1047* (DUKE); slopes above Golfito along trail to TV tower, elev. 100–300 m, *Burger & Matta 4769* (F, GH), *4771* (F, US); 12 km E of Golfito, *Harmon & Fuertes 6173* (MO); Golfito, near airport, elev. ca. 50 ft, *Kress 78-1048* (DUKE); 3.5 mi beyond Golfito, ca. sea level, *Kress et al. 76-586* (DUKE); 5 mi above Villa Neily on road to San Vito de Java, elev. 2100 ft, *Kress 78-1050* (DUKE); San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. 3900 ft, *Kress 76-576* (DUKE), *78-1032* (DUKE); Orillas de Mar de Golfito de Osa, *Brenes 12325a* (F); Península de Osa, 5 km W of Rincón de Osa, elev. 50–200 m, *Burger & Gentry 8977* (F), *Burger & Stolze 5469* (CR, F); 4 mi W of Rincón de Osa, near airport, elev. 100 ft, *Raven 21686* (CR, F, NY); Rincón, *Semple 80* (MO), *Sheffy 37* (CR). SAN JOSÉ/PUNTARENAS: between Playa Dominical, Baru, and Tinamastes along road to San Isidro del General, elev. 10–500 m, *Burger & Baker 10138* (F). SAN JOSÉ: along hwy. between Parrita and Santiago near Finca Los Angeles, *Kress & Cooper-Smith 76-634* (DUKE), elev. 2200 ft, *Kress et al. 77-799* (DUKE). **Panama.** CHIRIQUÍ: Península de Burica, 10 mi W of Puerto Armuelles, elev. 100–300 m, *Liesner 85* (F, MO, NY).

PHENOLOGY. Flowering mainly during early part of rainy season (June to September); some inflorescences produced all year.

HABITAT AND DISTRIBUTION. This species is often found on steep slopes in old secondary growth at elevations below 500 m. It is primarily restricted to the drier Pacific slopes and coastal plains of Costa Rica, from the area around Parrita south to the Burica Peninsula (MAP 6).

RELATIONSHIPS. *Heliconia stilesii* is most closely related to *H. curtispatha*, the only other Central American member of the *curtispatha* group. It differs from that species in its extremely flexuose rachis, in its strictly distichous, nearly imbricate cincinnal bracts, and in being mainly restricted to the Pacific slopes of Costa Rica.

FIGURE 11. *Heliconia stilesii*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, partially reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma. (© Museo Nacional de Costa Rica, 1982; reprinted with permission.)



NOMENCLATURE. Griggs (1915) and later Daniels & Stiles (1979) mistakenly applied the name *Heliconia curtispatha* Peterson to this taxon.

13. ***Heliconia sessilis*** Kress, J. Arnold Arbor. **62**: 251. 1981. TYPE: Panama, Colón, along road between Gatún Lock and Fort Sherman, elev. ca. 3 m, Kress 80-1241 (holotype, DUKE!; isotypes, F!, GH!, K! MO!, PMA!).

FIGURE 12; PLATE VI, A, C.

Heliconia pogonantha auct. non Cuf.: Croat, Fl. Barro Colorado Is. 257. 1978.

Herb with *Musa*-like habit, 6–7 m tall. Leafy shoots in groups of 10 to 20; pseudostem green to brown, glabrous, 2.5 m tall, 8–9 cm in diameter; leaves 4 or 5 per shoot; petiole olive green, glabrous, 1.4–1.8 m long, 2 cm in diameter; blade with the base unequal, attenuate to obtuse, the apex acute, the upper surface green, glabrous, with midrib olive green and glabrous, the lower surface dull green, glaucous, with midrib yellow-green with central maroon stripe and slightly glaucous, the longest blade 2 m by 40–60 cm. Inflorescence nodding to pendent, to 90 cm long; peduncle obscure, red, puberulous, 2 cm in diameter; rachis flexuose, red at base of inflorescence, yellow toward distal bracts, puberulous, 1.8–1.9 cm in diameter at base; cincinnal bracts spirally arranged, 23 to 30 per inflorescence, oriented 90° to axis of inflorescence, the basal bract usually sterile, the middle bract with apex acute, margins straight becoming involute near rachis, inner surface white to pink and glabrous to puberulous, the outer surface red and glabrous, 8–9 cm long, 9 cm wide at base, l/w = 0.9. Floral bracts opaque, persistent, pale yellow, pink along margins, puberulous abaxially, 3.5–4 cm long, 1.8–2.1 cm wide at base. Flowers 15 to 20 per cincinnus; pedicel white, reddish near ovary, glabrous, 6–10 mm long; perianth deep yellow distally, paler at base, glabrous except for puberulous sepal margins, 4.8–5.1 cm long, 1.1–1.2 cm wide at base, at anthesis curved 30–40° and slightly sigmoid; free sepal reflexed, fused sepals with apices reflexed; staminode white to pale yellow, 6–7 by 3 mm, apex cuspidate; stamens with anthers connivent inside apex of corolla tube; pollen medium size ($57 \times 79 \mu\text{m}$), euoblate (P/E = 0.72), subisopolar (DR/PR = 2.43), with the distal hemisphere subconvex, spinulose, the proximal hemisphere planar, psilate, the germination aperture distinct, flattened, sunken; ovary white becoming pale lavender around apex, glabrous, 1–1.2 cm by 6–7 mm. No mature fruits seen.

SPECIMENS EXAMINED. **Panama.** CANAL ZONE: vic. of Fort Sherman, W of Colón, near sea level, Kress & Clarkson 77-871 (DUKE), Standley 31117 (US); W of Limón Bay, Gatún Locks, and Gatún Lake, Johnston 1639 (GH); Barro Colorado Is., laboratory clearing, Croat 12422 (MO, NY, SCZ).

PHENOLOGY. Flowering during wettest part of rainy season (late August probably to December).

HABITAT AND DISTRIBUTION. This species is found in flooded secondary growth in the Atlantic coastal lowlands of Panama (MAP 7). Only a very localized population has been found west of Colón, but this species may be scattered farther east in Panama and even into South America.

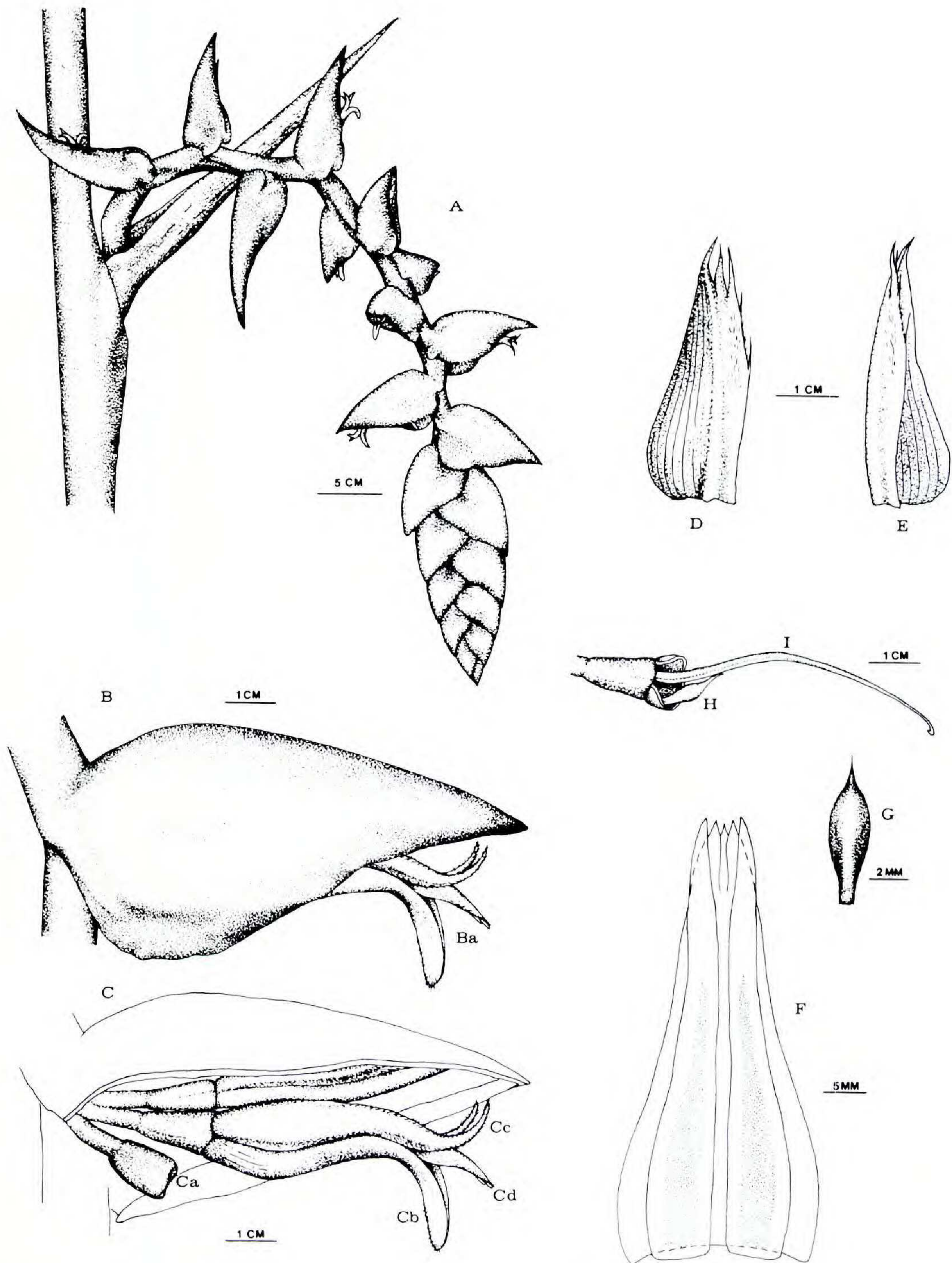
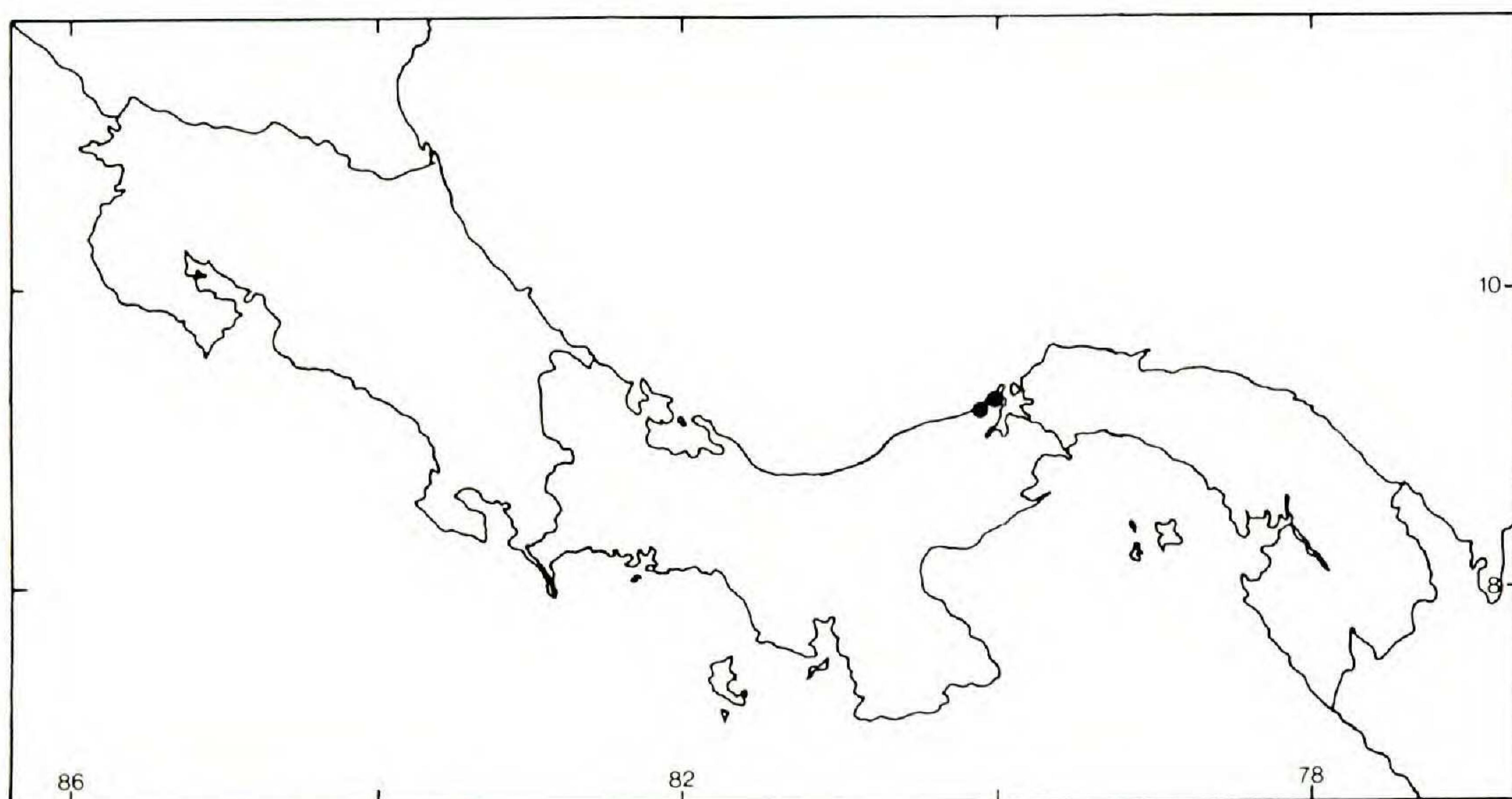


FIGURE 12. *Heliconia sessilis*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma.



MAP 7. Costa Rica and Panama, showing restricted distribution of *Heliconia sessilis*.

RELATIONSHIPS. *Heliconia sessilis* is allied to members of the *curtispatha* and *pogonantha* groups with large, leafy shoots and massive inflorescences. However, it most likely belongs to a separate lineage that is made up primarily of taxa found in South America. This species is characterized by its semiaquatic habitat, its attenuate leaf bases, its sessile inflorescences, and its only slightly sigmoid perianths.

14. ***Heliconia mariae*** J. D. Hooker, J. Proc. Linn. Soc., Bot. 7: 69. 1864. TYPE: New Granada [Colombia], Bolivar, Betami on the Sinu River (lat. 8° N), *A. Anthoine* s.n., 1859 (holotype, K!). PLATE VI, B, D.

Bihai mariae (J. D. Hooker) Kuntze, Rev. Gen. Pl. 2: 684. 1891.

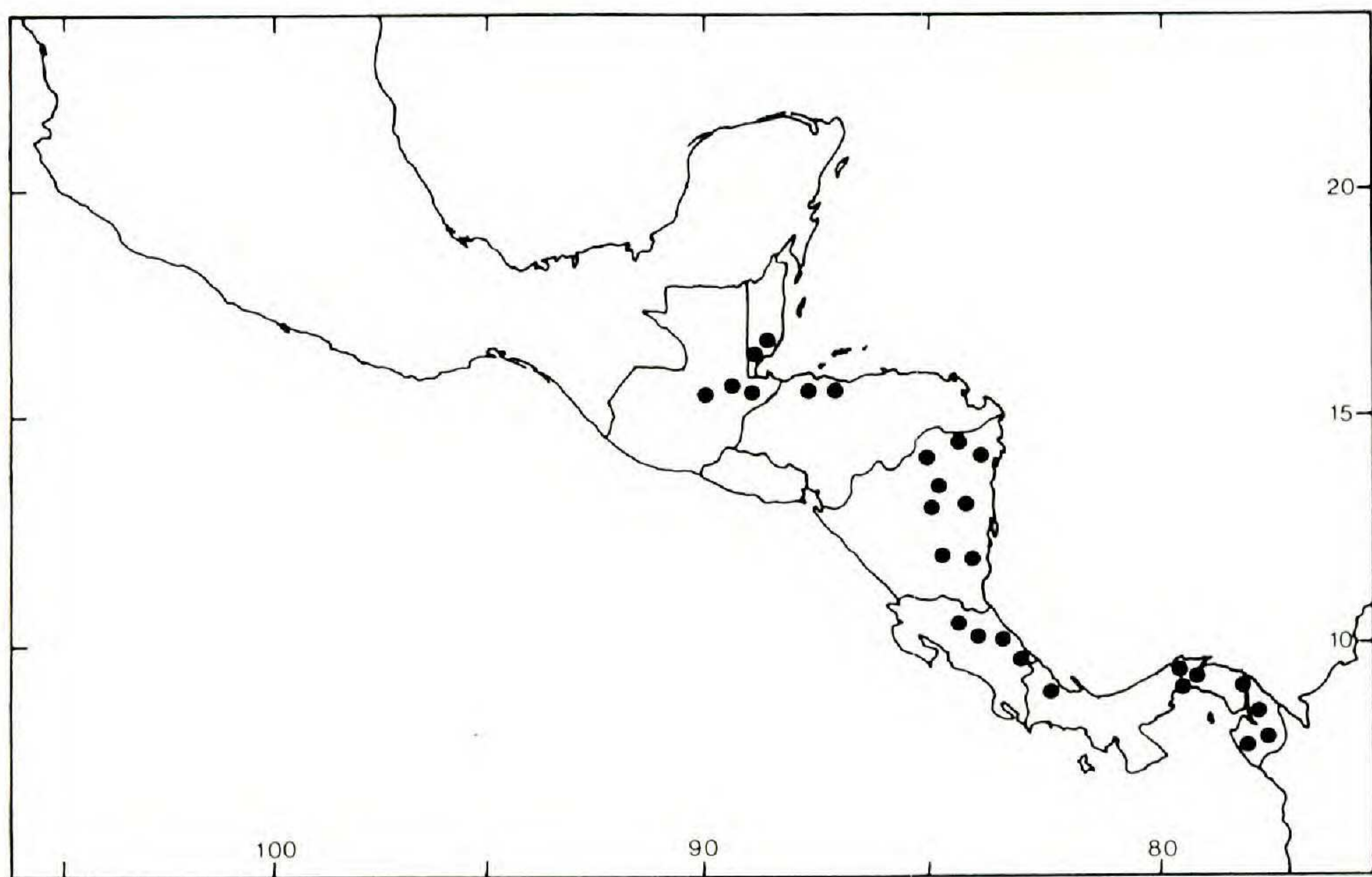
Heliconia elegans Petersen in Martius & Eichler, Fl. Brasil. 33: 12. 1890. *Bihai elegans* (Petersen) Kuntze, Rev. Gen. Pl. 2: 684. 1891. TYPE: Panama, [Canal Zone,] Paraiso, *M. Wagner* s.n., Dec. 1857 (holotype, M!).

Bihai punicea Griggs, Bull. Torrey Bot. Club 42: 321. 1915. *Heliconia punicea* (Griggs) L. B. Smith, Contr. Gray Herb. 124: 6. 1939. TYPE: Panama, Canal Zone, between Gorgona and Gatún, elev. 10–50 m, *Pittier* 2290 (holotype, US!).

Herb with *Musa*-like habit, 4–7.5 m tall. Leafy shoots in groups of 5 to 30; pseudostem red-green, glabrous, 1.9–3.8 m tall, 6–10 cm in diameter; leaves 4 to 6 per shoot; petiole green to yellow-green, often with brown spots, glabrous, 0.9–1.7 m long, 1.5–2.5 cm in diameter; blade with the base unequal, truncate, the apex obtuse to acute, the upper surface green to dark green, glabrous, with midrib light green and glabrous, the lower surface green, glabrous to slightly glaucous, midrib yellow-green with maroon midstripe and glabrous, the longest blade 1.7–2.5 m by 45–65 cm. Inflorescence pendent, long lived, to 65 cm long; peduncle red to yellow-red, densely scurfy, 20–70 cm long, 1.4–1.8 cm in diameter; rachis slightly flexuose, red to yellow, glabrous to scurfy, 1.5–1.8 cm in diameter at base; cincinnal bracts distichous, 40 to 65 per inflorescence, oriented 90–100° to axis of inflorescence, the basal bract usually fertile, the

middle bract with apex acute, margins straight, inner surface white to pink and glabrous, outer surface pink to red (becoming yellowed with age) and glabrous to scurfy, 4.5–6.5 cm long, 7.5–9 cm wide at base, $l/w = 0.7$. Floral bracts opaque, persistent, white, glabrous to puberulous abaxially, 4–5 cm long, 1.5–2.5 cm wide at base. Flowers 20 to 30 per cincinnus; pedicel white to pink, glabrous to puberulous, 8–15 mm long; perianth white and glabrous basally, pink to red and puberulous apically, 3–4 cm long, 5–6 mm wide at base, at anthesis curved 40–70°, parabolic; free sepal slightly reflexed, fused sepals with apices reflexed; staminode white, 5–7 by 2–3 mm, apex acute to acuminate; stamens with anthers connivent inside perianth apex; pollen *pogonantha* type, medium size ($56 \times 76 \mu\text{m}$), euoblate ($P/E = 0.74$), heteropolar ($DR/PR = 6.84$) with the distal hemisphere convex (sometimes truncate), spinulose, the proximal hemisphere planar to subconvex, psilate, the germination aperture distinct, flattened and sunken; ovary white, glabrous, 6–9 by 5–6 mm. Drupes glabrous, 1–1.2 cm by 7–9 mm wide.

SPECIMENS EXAMINED. **Belize.** TOLEDO: Columbia Forest Reserve, ca. 1–2 mi N of entrance, *Croat 24153* (MO); along Aguacate Rd. 0.5 mi from junction with San Antonio road, *Proctor 35858* (MO); Big Fall Estate, Caliente, elev. 20 m, *Whitefoord 1560* (BM). DISTRICT UNKNOWN: Fairview, elev. 200 ft, *Schipp 8413* (F). **Guatemala.** ALTA VERAPAZ: Finca Sepacuite, *Cook & Griggs 787* (US); 28 mi from Tactic on road to El Estor, elev. 650 ft, *Kress et al. 77-745* (DUKE). IZABAL: 6–8 km S of Modesto Méndez, elev. 110 m, *Harmon 2551* (MO); 70 mi from Flores, just below San Luís de Petén, elev. 1000 ft, *Kress et al. 77-743* (DUKE); jungle bordering Quebrada Roséul, lower slopes bordering E part of Cerro Santa Cruz, NE of San Filipe, elev. 50–150 m, *Steyermark 39638* (F). **Honduras.** ATLÁNTIDA: Lancetilla valley near Tela, N Coast, *Pfeifer 2115* (US); vic. of Tela at sea level, *Standley 53745* (F, US); on slopes near Puente Alto stop on S.F. Co. R.R. E of Ceiba, elev. 900 ft, *Yuncker et al. 8529* (F, GH, NY); Puerto Sierra, near Highland Creek, *Wilson 307* (NY, US). **Nicaragua.** COMARCA DEL CABO: Miguel Bikou, *Robbins 5863a* (MO). JINOTEGA: Salto Acatula, Río Bocay, elev. 130 m, *Stevens et al. 16758* (MO); Valle del Cuá, El Cedro, elev. 700 m, *Moreno 843* (MO), 962 (MO). MATAGALPA: slope of Cerro Musun, Quebrada El Jobo (tributary of Río Paiwas), elev. ca. 300 m, *Stevens 12012* (MO). ZELAYA: Bluefields, Cerro Maypita, 4 km ENE of Rama, elev. ca. 150 m, *Proctor et al. 27357* (F, NY); forest near Yauya, ca. 18 km SE of La Lux, elev. 150–200 m, *Bunting & Licht 579* (F, NY); 40 mi W of Rama, elev. 300 ft, *Kress et al. 77-761* (DUKE); along trail from Cerro Saslaya to San José del Hormiguero, from Loma Mollejones E, halfway to San José del Hormiguero, elev. ca. 200–400 m, *Stevens 7023* (DUKE); vic. of San José del Hormiguero, elev. ca. 120–150 m, *Stevens 7169* (DUKE); about 8–9 km E of Río Kukalaya on road from Puerto Cabezas to Rosita, elev. 200–300 m, *Stevens 8695* (DUKE); Kururia, elev. 50 m, *Pipoly 3984* (MO); Waylawás, elev. 90–200 m, *Pipoly 4197* (MO), 4343 (MO). **Costa Rica.** ALAJUELA: forest near Cerro Negro and along road 18–22 km N of Aguas Zarcas in Llanura de San Carlos, elev. 60 m, *Burger & Stolze 5170* (F); along road between Jabillos and La Fortuna, elev. 600 ft, *Kress et al. 77-771* (DUKE); Llanura de San Carlos, elev. 100 m, *Molina et al. 17657* (F, NY, US). CARTAGO: forêts de Peralta, vallée du Reventazón, elev. 250 m, *Pittier 2360* (K). HEREDIA: Finca La Selva, elev. 100 m, *Kress & Cooper-Smith 76-524* (DUKE); Finca La Selva, W River Road, elev. 100 m, *Kress 79-1104* (DUKE). LIMÓN: along hwy. from Turrialba to Siquirres NE of Chitaria, *Sheffy 36* (CR); near Moín along hwy. to Limón, elev. 25 m, *Kress & Cooper-Smith 76-619* (DUKE); along road between Puerto Viejo and BriBri, elev. 300 ft, *Kress et al. 77-794* (DUKE); road between BriBri and Bratsi, along Río Sixaola, elev. 10–50 m, *Burger et al. 10456* (F). PUNTARENAS: Las Cruces Trop. Bot. Garden, cult., elev. 3500 ft, *Kress 78-1022* (DUKE). PROVINCE UNKNOWN: near Platanillo, Toro Amarillo,



MAP 8. Mexico and Central America, showing distribution of *Heliconia mariae*.

Folis 23914 (CR); elev. 31 m, *Tónduz* 14551 (CR). **Panama.** BOCAS DEL TORO: vic. of Chiriquí Lagoon, *Von Wedel* 2905 (GH, MO). CANAL ZONE: Barro Colorado Is., *Croat* 6568 (MO), *Croat* 8689 (MO); along K16C, vic. of Certo Viejo, *Blum* 1274 (scz); Río Providencia and ridge S of river, elev. 5–170 m, *Nee & Gentry* 8714 (MO, PMA); old site of Gorgona, *Maxon* 6784 (US); hills near Huile around Gatún Lake, *Smith et al.* 3292 (F, US); Empire to Mandingo, *Piper* 5437 (US); Cerro Gordo near Culebra, *Standley* 26000 (US); hills near Gatún, *Standley* 27234 (US); between Gorgona and Gatún, elev. 10–50 m, *Pittier* 2290 (US); Pipeline Road, elev. ca. 75 m, *Kress & Cooper-Smith* 76-644 (DUKE), *Kress et al.* 77-855 (DUKE), *Wilbur & Weaver* 11272 (DUKE); along R.R. and Panama Canal, 6 km W of Gamboa, elev. 30–40 m, *Nee* 7213 (MO). COLÓN: ridge behind Garotte, *D'Arcy* 9323 (US); road between Ft. Sherman and Margarita, elev. 25 ft, *Kress & Clarkson* 80-1146 (DUKE); camino hacia San Lorenzo después de Fort Sherman, *Quistgaard* 3 (PMA); Río Guanche, elev. 0–50 ft, *Antonio* 4821 (MO). DARIÉN: Bayano Dam Bridge, elev. 50 ft, *Antonio* 4517 (MO); vic. of Boca de Cupe, elev. ca. 40 m, *Allen* 879 (MO); Punta Guayabo Grande, elev. 0–50 m, *Antonio & Hahn* 4249 (MO); between Río Jesús and Sabado, elev. ca. 100 ft, *Hammel* 1347 (MO); Quebrada Camachi muricate cerca casa de Bartoc, *Kennedy* 2831 (MO); tributary Río Correlón, *Sexton* 211 (MO). PANAMÁ: Río Espave, *Gentry* 3790 (MO, PMA); 3 km S of Alcalde Díaz, elev. 410–440 m, *Nee* 8554 (MO). SAN BLAS: Playón Chico and vic. of San Blas, Tappakanti, *Stier* 167 (MO); Sasardi, elev. 20 m, *Duke* 10119 (NY). PROVINCE UNKNOWN: Tabernilla, *Cowell* 272 (NY); Matachin, *Kuntze s.n.*, Aug. 1869 (NY).

PHENOLOGY. Inflorescences very long lived (up to 8 months) from first flowering to fruiting; most plants with inflorescences in various stages all year.

HABITAT AND DISTRIBUTION. This species is found from Belize to Panama and extends into northern South America (MAP 8). It inhabits open secondary growth from sea level to 500 meters on both Atlantic and Pacific coasts, being more abundant on the wetter, Caribbean side. Plants of *Heliconia mariae* are soon shaded out in later successional stages and are almost never found in primary forest habitats.

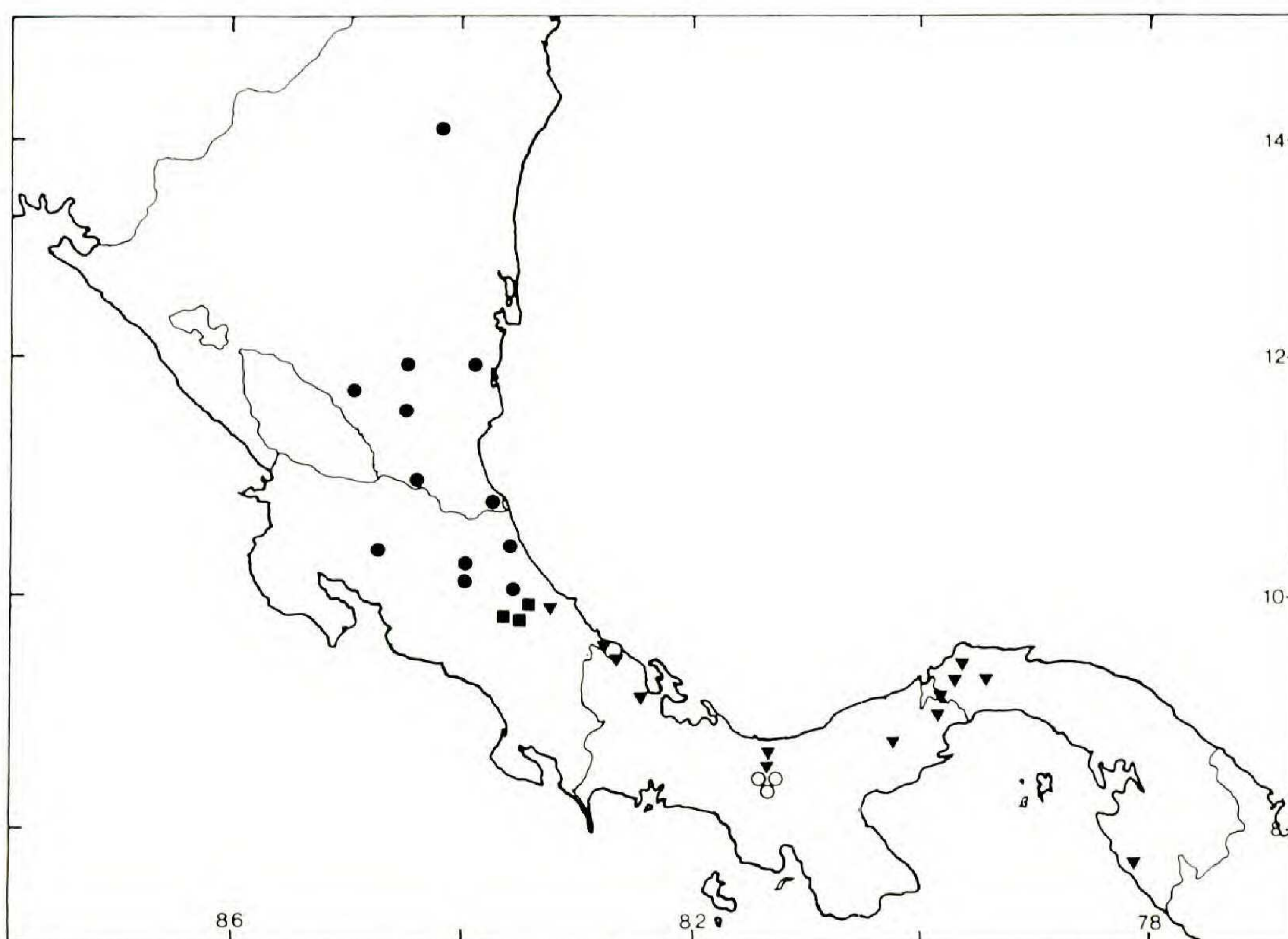
RELATIONSHIPS. *Heliconia mariae* is a member of the *pogonantha* group, but it has several characters derived within that group, including strictly distichous cincinnal bracts, parabolic flowers with red, puberulous perianths less than 4 cm in length, and pollination by territorial nonhermit hummingbirds.

15. ***Heliconia pogonantha*** Cuf. Arch. Bot. Sist. **9**: 191. 1933. TYPE: Costa Rica, in regione Atlantica, in selva densa ad rivum prope "La Castilla-Los Negritos," 12 km ab ore fluminis Reventazon, *Cufodontis* 621 (w) (type destroyed in World War II; Field Museum photograph (Neg. 30912!) remains). NEOTYPE: Costa Rica, Heredia, Puerto Viejo, Finca La Selva, *Daniels & Stiles* 14 (F!).

Herb with *Musa*-like habit, 4–7.5 m tall. Leafy shoots in groups of 2 to 20; pseudostem glabrous to scurfy, 1.3–4 m tall, 5–10 cm in diameter; leaves 3 to 6 per shoot; petiole light green to yellow-green, glabrous, 1.1–1.8 m long, 1.5–3 cm in diameter; blade with the base unequal, truncate to cordate, the apex acute, the upper surface dark green, glabrous, with midrib green to yellow-green and glabrous, the lower surface light green to green, slightly glaucous, with midrib yellow-green and maroon and slightly glaucous to scurfy, the longest blade 1.2–3.3 m by 40–65 cm. Inflorescence pendent, to 1.6 m long; peduncle red to yellow, puberulous to woolly, 10–60 cm long, 1.7–2.7 cm in diameter; rachis flexuose, red to yellow, puberulous to velutinous, 1.4–2.5 cm in diameter at base; cincinnal bracts usually spirally arranged, 20 to 55 per inflorescence, oriented 100–145° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex acute to acuminate, margins straight to involute at base, inner surface yellow to red and puberulous to velutinous, outer surface red (sometimes yellow near rachis) and glabrous to velutinous, 8–12.5 cm long, 9–16 cm wide at base, $l/w = 0.8$. Floral bracts opaque, persistent, white to yellow, tomentose to velutinous with golden hairs abaxially, 5–7 cm long, 1.5–2.5 cm wide at base. Flowers 10 to 30 per cincinnus; pedicel white to yellow to pink, glabrous to puberulous, 7–16 mm long; perianth yellow, glabrous basally, velutinous with golden hairs toward apex, 5–6 cm long, 9–12 mm wide at base, at anthesis curved 45–90° and sigmoid; free sepal slightly reflexed, fused sepals with apices reflexed; staminode white, yellow at apex, 5–9 by 2–3 mm, apex acuminate; stamens with anthers connivent inside apex of corolla tube; pollen *pogonantha* type, large ($60\text{--}65 \times 75\text{--}86 \mu\text{m}$), euoblate (to sometimes suboblate) ($P/E = 0.71\text{--}0.84$), heteropolar ($DR/PR = 6.15\text{--}8.08$) with the distal hemisphere convex, truncate, spinulose, the proximal hemisphere planar, psilate, the germination aperture distinct, flattened, sunken; ovary white, glabrous, 8–12 by 5–8 mm. Drupes glabrous.

DISTRIBUTION. *Heliconia pogonantha* is widespread in the Neotropics. In Central America (MAP 9) the four geographically distinct varieties generally inhabit moist forested slopes and often invade disturbed open areas from sea level to 1000 m.

VARIATION. The four Central American varieties of *Heliconia pogonantha* differ from each other in inflorescence vestiture and color and in overall size. Additional geographic variants of this species are found in South America.



MAP 9. Nicaragua, Costa Rica, and Panama, showing distribution of *Heliconia pogonantha*: var. *pogonantha* (solid circles), var. *holerythra* (solid triangles), var. *pubescens* (solid squares) and var. *veraguasensis* (open circles).

RELATIONSHIPS. This species is closely related to *Heliconia ramonensis* and other members of the *pogonantha* group. The taxa of this group differ from other heliconias with pendent inflorescences in the usually velutinous to woolly peduncles, rachises, cincinnal bracts, and perianth apices, and in the large pollen grains with flattened, sunken germination apertures. Three of the four Central American varieties of *H. pogonantha* have essentially glabrous inflorescences and are therefore readily distinguished from other members of the *pogonantha* group.

NOMENCLATURE. The neotype of *Heliconia pogonantha* selected by Daniels and Stiles (1979) is in accordance with the protologue provided by Cufodontis. However, the Field Museum photograph of the original type specimen destroyed in World War II is certainly adequate for the correct identification of the species. The necessity for neotypification is therefore questionable.

Key to the Varieties of *Heliconia pogonantha*

- A. Inflorescence entirely red. 15b. var. *holerythra*.
- A. Inflorescence red and yellow.
 - B. Peduncle, rachis, and cincinnal bracts velutinous to woolly. 15c. var. *pubescens*.
 - B. Peduncle, rachis, and cincinnal bracts glabrous to puberulous.
 - C. Plants less than 5 m in height; lower surface of leaf blade maroon tinted;

- cinnal bracts oriented 115–135° to axis of inflorescence at maturity. 15d. var. *veraguasensis*.
 C. Plants greater than 5 m in height; lower surface of leaf blade green; cinnal bracts oriented 100–120° to axis of inflorescence at maturity. 15a. var. *pogonantha*.

15a. *Heliconia pogonantha* var. *pogonantha*

Herb 5–7 m tall. Leafy shoots in groups of 3 to 11; pseudostem bronzy green, glabrous, 2–4 m tall, 6–8 cm in diameter; leaves 4 or 5 per shoot; petiole light green to green, 1.3–1.8 m long, 2–3 cm in diameter; longest blade 2.4–3.3 m by 41–62 cm. Inflorescence to 1.5 m long; peduncle puberulous to scurfy, 25–55 cm long, 1.8–2.7 cm in diameter; rachis yellow, puberulous to scurfy, 1.4–2.5 cm in diameter at base; cinnal bracts 25 to 55 per inflorescence, oriented 100–120° to axis of inflorescence, the middle bract with margins straight to involute at base, inner surface yellow to pink and velutinous with golden hairs, outer surface red becoming yellow near rachis and puberulous to scurfy, 8–9.5 cm long, 9.5–12 cm wide at base. Floral bracts tomentose to velutinous with golden hairs abaxially, 4–5 cm long, 1.7–2.5 cm wide at base. Flowers 15 to 30 per cincinnus; pedicel pale yellow, glabrous, 9–12 mm long; perianth 5–5.8 cm long, 9–11 mm wide at base, at anthesis curved 45–70°; staminode 7–9 by 2–3 mm; ovary 1–1.1 cm by 6–8 mm.

SPECIMENS EXAMINED. **Nicaragua.** CHONTALES: ca. 4.5 km S of Hwy. 7 on road to Nueva Guinea, elev. ca. 200 m, *Stevens 4949* (DUKE). RÍO SAN JUAN: near Caño Chontaleño, 20 km NE of El Castillo (Río Indio watershed), elev. 200 m, *Neill 3425* (DUKE); in forest along Río San Juan between San Juan del Norte (Greytown) and Delta de San Juan, elev. 0–50 m, *Bunting & Licht 883* (F, NY). ZELAYA: Bluefields, summit and slopes of Cerro San Isidro, elev. 0–65 m, *Proctor et al. 27292* (F, NY); 20 mi W of Rama, elev. 200 ft, *Kress et al. 77-760* (DUKE); along road to Colonia Yolaina, Colonia La Esperanza, ca. 1.3 km SE of intersection with road between Nueva Guinea and Colonia Verdún, elev. 180–200 m, *Stevens 6349* (MO); along road between Río Blanco and Río Copalar, elev. 200–400 m, *Stevens 12100* (DUKE, MO); 8 km E of bridge E of Rosita on road to Bonanza, elev. 90 m, *Stevens 12594* (DUKE, MO); Bonanza, elev. 250–350 m, *Stevens 18793* (MO). **Costa Rica.** GUANACASTE: below Volcán Tenorio, elev. 700 ft, *Kress 80-1218* (DUKE). HEREDIA: Finca La Selva, elev. 100 m, *Burger & Stolze 5785* (CR, F, GH, NY), *Kress 76-523* (DUKE), *79-1102* (DUKE), *Sheffy 53* (CR); near Tirimbina, E of Río Sarapiquí, elev. 150–250 m, *Burger & Burger 8123* (F); near Puerto Viejo along road near Río Sucio, elev. 20 m, *Croat 35722* (MO); La Virgen, along Río San Ramón, elev. 650 ft, *Kress et al. 77-778* (DUKE). LIMÓN: N end of Tortuguero Park, elev. 0–30 m, *Burger & Antonio 11222* (F); La Suerte, W of Tortuguero, elev. 40 m, *Davidson & Donahue 8558* (GB); Finca Montecristo, on Río Reventazón below Cairo, elev. 25 m, *Standley & Valerio 48984* (US). PUNTARENAS: Península de Osa, 5 km W of Rincón de Osa, elev. 50–200 m, *Burger & Gentry 9259* (F); San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. ca. 4000 ft, *Kress 76-569* (DUKE), *Kress 78-1028* (DUKE). PROVINCE UNKNOWN: lieux humides à Lent, elev. 31 m, *Tónduz 14542* (photo, MO).

PHENOLOGY. Flowering primarily during dry and early rainy seasons (January to August); some inflorescences produced nearly all year.

HABITAT AND DISTRIBUTION. *Heliconia pogonantha* var. *pogonantha* is restricted to the wet Atlantic lowlands below 300 m in Nicaragua and Costa Rica

north of Limón (MAP 9). This variety is found in wooded late secondary growth and often develops large stands in light gaps and along forest margins.

15b. ***Heliconia pogonantha* var. *holerythra*** Daniels & Stiles, *Brenesia* 15(Supl.):

39. 1979. TYPE: Costa Rica, Limón, Río Sand Box, 2 km NE of BriBri, *Baker & Burger* 80 (holotype, F!).

Herb 4.5–7.5 m tall. Leafy shoots in groups of 2 to 18; pseudostem 1.4–2.6 m tall, 7–10 cm in diameter; leaves 3 to 6 per shoot; petiole 1.1–1.8 m long, 2–3 cm in diameter; longest blade 2–2.3 m by 40–65 cm. Inflorescence to 1.6 m long; peduncle red, scurfy, 20–60 cm long, 1.7–2.5 cm in diameter; rachis red, scurfy, 2–2.5 cm in diameter at base; cincinnal bracts 30 to 40 per inflorescence, oriented 120–140° to axis of inflorescence, the middle bract with apex acute to acuminate, often necrotic, margins straight (sometimes necrotic), inner surface puberulous, outer surface red and puberulous to scurfy, 10–12.5 cm long, 11–16 cm wide at base. Floral bracts tomentose to velutinous abaxially, 5–7 cm long, 2–2.5 cm wide at base. Flowers 15 to 30 per cincinnus; pedicel white to pink, glabrous, 1.2–1.6 cm long; perianth white to pink basally, yellow at apex, 5–5.7 cm long, 1–1.2 cm wide at base, at anthesis curved 75–85°; staminode 6–8 by 3 mm; ovary white (sometimes slightly maroon), 9–10 by 6–7 mm. Drupes 1.5–2 by 1–1.3 cm.

SPECIMENS EXAMINED. **Costa Rica.** ALAJUELA: 38 km from Interamerican Hwy. toward Upala, *Wilbur* 20062 (DUKE). LIMÓN: 5–15 km from Siquirres on new road to Limón, elev. 50–100 m, *Baker & Burger* 184 (DUKE, F); Cimarrones, E of Siquirres, elev. 200 m, *Maas* 1134 (U); 1–3 km N of BriBri, Río Sixaola Drainage, elev. 20–200 m, *Burger & Antonio* 10981 (F); between Puerto Viejo and BriBri, elev. ca. 300 ft, *Kress et al.* 77-790 (DUKE). **Panama.** BOCAS DEL TORO: top of second fila above Almirante, *Gentry* 2813 (F, MO, NY). CANAL ZONE: along Transisthmian Hwy., 10 km from Colón turnoff, elev. ca. 300 ft, *Kress & Clarkson* 80-1150 (DUKE); Pipeline Road, *Andersson & Sytsma* 1233 (GB, S); along Río Mendosa near Pipeline Road bridge, 8 km NW of Gamboa, elev. 95 m, *Nee* 7742 (US). COCLÉ: above La Pintada on road to Coclecito, elev. 1600–1700 ft, *Kress et al.* 80-1164 (DUKE). COLÓN: E Santa Rita Ridge lumber road, *Correa & Dressler* 619 (SCZ); Santa Rita Hills, *C. E. Smith & H. M. Smith* 3447 (F, US); Santa Rita Ridge, *Gentry & Dwyer* 9550 (MO); Santa Rita, 4 km desviación de la Transisthmica, Cuadro 1, elev. 150 m, *Gómez-Pompa et al.* 3222 (MO, PMA); near Guasimo along river, *Croat* 9954 (MO); Río Guanche, elev. ca. 25 m, *Kress & Cooper-Smith* 76-658 (DUKE); Río Buenaventura, 3 mi from Portobelo, ca. sea level, *Kress et al.* 77-874 (DUKE); below Cerro Bruja, elev. 600–700 m, *Andersson & Sytsma* 1240 (GB, MO, S). DARIÉN: trail from Punta Guayabo Grande to Río Jaqué, elev. 50–200 m, *Antonio & Hahn* 4385 (MO). PANAMÁ: Alto de Pacora below Cerro Jefe, elev. 800–900 m, *Kress et al.* 76-636 (DUKE); El Llano–Cartí Road, elev. 1600 ft, *Kress & Hammel* 82-1334 (DUKE). VERAGUAS: valley of Río Dos Bocas on road between Alto Piedra (above Santa Fé) and Calovébora, elev. 350–400 m, *Croat* 27390 (MO); valley of Río Dos Bocas, 11 km from Escuela Agrícola Alto Piedra above Santa Fé on road to Calovébora, elev. 450 m, *Croat* 27515 (MO); Atlantic slope, beyond Santa Fé on road to Calovébora, elev. 1200 ft, *Kress et al.* 80-1199 (DUKE).

PHENOLOGY. Flowering primarily during dry and early rainy seasons (January to August).

HABITAT AND DISTRIBUTION. This variety is found on the Atlantic slopes and coastal plains of Costa Rica and Panama from Limón to Darién, extending

into South America (MAP 9). It is most common at elevations from sea level to 200 m but occurs to over 800 m. Variety *holerythra* prefers open disturbed habitats, often near streams or rivers.

RELATIONSHIPS. Variety *holerythra* differs from other varieties of *Heliconia pogonantha* in its greater overall stature, its puberulous to scurfy, entirely red inflorescences, and its large, heavy cincinnal bracts.

- 15c. ***Heliconia pogonantha* var. *pubescens*** Daniels & Stiles, Brenesia 15(Supl.): 37. 1979. TYPE: Costa Rica, [Limón,] Turrialba–Siquirres road, 840 m elev., *Daniels & Stiles* 40 (holotype, F!).

Herb 5–7 m tall. Leafy shoots in groups of 8 to 20; pseudostem 1.8–2.7 m tall, 6–7 cm in diameter; leaves 3 to 5 per shoot; petiole 1.3–1.6 cm long, 2–2.5 cm in diameter; longest blade 2–2.7 m by 45–55 cm. Inflorescence to 1.5 m long; peduncle yellow to red, woolly with yellow hairs, 30–55 cm long, 1.5–2.2 cm in diameter; rachis yellow to red, densely velutinous with yellow hairs, 1.5–2.1 cm in diameter at base; cincinnal bracts 25 to 35 per inflorescence, oriented 140–145° to axis of inflorescence, the middle bract with margins straight, inner surface pale yellow to orange and velutinous, outer surface red distally becoming yellow near rachis and velutinous, 9–10 cm long, 9–13 cm wide at base. Floral bracts 5.5 cm long, 2 cm wide at base. Flowers 15 to 25 per cincinnus; pedicel white to pink, glabrous, 1.2 cm long; perianth 6 cm long, 8–12 mm wide at base, at anthesis curved 70–90°; staminode 5–7 by 2–3 mm; ovary 1–1.2 cm by 6–7 mm. Drupes 1.5–1.7 cm by 9–11 mm.

SPECIMENS EXAMINED. **Costa Rica.** CARTAGO/LIMÓN: along road between Turrialba and Siquirres, elev. 2000–2500 ft, *Kress et al.* 77-788 (DUKE). CARTAGO: road from Turrialba N to Pavones and Siquirres, elev. 600–700 m, *Lems* 5054 (NY, US); beside Río Tepemechin, 4 km SE of Pejibaye, elev. 650 m, *Lent* 3192 (F); forest near Río Tepemechin, elev. 800 m, *Lent* 3737 (F); Chitaria, elev. 900 m, *Maas* 755 (F). LIMÓN: along Hwy. 32 from Turrialba to Limón, ca. 11 mi S of Siquirres, elev. 650 m, *Croat* 43326 (MO); near Guayacán, elev. 700 m, *Kress* 76-611 (DUKE); along Hwy. CR 233, 15 km N of Tres Equis, elev. 300 m, *Lent* 528 (F); Cimarrones, ca. 10 km E of Siquirres, margin of forested valley, elev. 200 m, *Maas* 1134 (F, MO); along hwy. from Turrialba to Siquirres, *Sheffy* 35 (CR); along hwy. to Siquirres near Chitaria, *Sheffy* 89 (CR).

PHENOLOGY. Flowering throughout year; peaking late in dry season (February to April).

HABITAT AND DISTRIBUTION. Similar to the typical variety, var. *pubescens* is found in secondary growth and along forest margins. This variety is restricted to the Atlantic foothills in Costa Rica between Turrialba and Siquirres at elevations of 200–800 m (MAP 9).

RELATIONSHIPS. The velutinous to woolly peduncle, rachis, and cincinnal bracts distinguish var. *pubescens* from the other varieties of *Heliconia pogonantha*.

- 15d. ***Heliconia pogonantha* var. *veraguasensis*** Kress, J. Arnold Arbor. 62: 256. 1981. TYPE: Panama, Veraguas, 2 mi above Santa Fé beyond Agricultural School, elev. 850 m, *Kress, Clarkson, & McDade* 77-825 (holotype, DUKE!; isotypes, K!, MO!).

PLATE VII, A, C.

Herb 4–4.5 m tall. Leafy shoots in groups of 3 to 15; pseudostem 1.3–1.7 m tall, 5 cm in diameter; petiole 1–1.2 m long, 1.5–1.8 cm in diameter; leaf blade with lower surface green tinted with maroon especially along margins, longest blade 1.2–1.5 m by 40–45 cm. Inflorescence to 75 cm long; peduncle yellow, scurfy to villous, 10–30 cm long, 1.8–2 cm in diameter; rachis yellow, puberulous to villous, 1.8–1.9 cm in diameter at base; cincinnal bracts 20 to 25 per inflorescence, oriented 115–135° to axis of inflorescence, the middle bract with margins straight, inner surface red-yellow and tomentose, outer surface red becoming yellow near rachis and glabrous to puberulous, 9–10.5 cm long, 8–9 cm wide at base. Floral bracts pale yellow, tomentose to velutinous with golden hairs abaxially, 4–4.8 cm long, 1.5–2.5 cm wide at base. Flowers 10 to 15 per cincinnus; pedicel white to yellow, puberulous, 7–12 mm long; perianth 5.4–5.7 cm long, 1–1.1 cm wide at base, at anthesis curved 80–90°; staminode 6–7 by 3 mm; ovary 8–9 by 5–6 mm.

SPECIMENS EXAMINED. **Panama.** VERAGUAS: vic. of Santa Fé, forested slopes of Cerro Tute, elev. 3000 ft, *Allen 4333* (MO); road between Santa Fé and Río Calovébora, 1.8 mi beyond Escuela Agrícola Alto Piedra, elev. 735 m, *Croat & Folsom 34255* (MO); shoulder of Cerro Tute, *Folsom & Edwards 3355* (MO); Cerro Tute, elev. 800–1350 m, *Knapp & Dressler 5438* (MO), *Sytsma & Antonio 2983* (MO), *Andersson & Sytsma 1277* (GB, s); beyond Escuela Agrícola, above Santa Fé, elev. 2600 ft, *Kress & Cooper-Smith 76-655* (DUKE), *76-656* (DUKE), elev. 2800–4600 ft, *Kress et al. 80-1189* (DUKE); beyond Santa Fé along road to Calovébora, Pacific slopes, elev. 2200 ft, *Kress et al. 80-1200* (DUKE), *Andersson & Sytsma 1288* (GB, s); lower montane wet forest 7 km W of Santa Fé, elev. 2900 ft, *Nee 11207* (US); Caribbean slope above Río Primero Brazo, *Liesner 959* (MO); Río Secundo Brazo, elev. 600–750 m, *Knapp & Dressler 5372* (MO), *Maas & Dressler 1673* (U).

PHENOLOGY. Flowering March to September; during most of year at least a few individuals reproductive.

HABITAT AND DISTRIBUTION. *Heliconia pogonantha* var. *veraguasensis* is known only from middle-elevation (735–1000 m) wet forests and secondary growth in the vicinity of Cerro Tute on the Pacific slopes in Veraguas, Panama (MAP 9).

RELATIONSHIPS. Variety *veraguasensis* is distinguished by its highly reflexed cincinnal bracts, its lower leaf surfaces tinted with maroon, and its overall stature smaller than in other varieties of *Heliconia pogonantha*.

16. ***Heliconia ramonensis*** Daniels & Stiles, *Brenesia* **15**(Supl.): 39. 1979. TYPE: Costa Rica, [Alajuela,] La Balsa, 11 mi N of San Ramón, elev. 1000 m, *Daniels, Kress, & Hutchison 111* (holotype, F!; isotypes, CR, US).

PLATE VII, C, D.

Herb with *Musa*-like habit, 4–6 m tall. Leafy shoots in groups of 2 to 10; pseudostem green to yellow to brown, glabrous to villous, 1–2 m tall, 4.5–8 cm in diameter; leaves 3 to 5 per shoot; petiole rusty green to green, glabrous, 1–1.8 m long, 1.1–2 cm in diameter; blade with the base unequal, obtuse to cordate, the apex acute to acuminate, the upper surface dark green, glabrous,

with midrib light green to yellow-green and glabrous, the lower surface green to maroon, glabrous, with midrib green to maroon and glabrous, the longest blade 1–2 m by 30–60 cm. Inflorescence pendent, to 90 cm long; peduncle pink to rose-red to red, glabrous to woolly with golden or rusty orange hairs, 20–60 cm long, 1.3–2 cm in diameter; rachis flexuose, red to pink to yellow, glabrous to woolly, 1–2.2 cm in diameter at base; cincinnal bracts distichous to subspirally arranged, 20 to 40 per inflorescence, oriented 120–140° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex acute to acuminate, margins straight to involute at base, inner surface pink to red to yellow and velutinous to villous with golden or rusty hairs, outer surface red to rose-red to pink and glabrous to woolly, 7–12 cm long, 7–10 cm wide at base, l/w = 1.1. Floral bracts opaque, persistent, white to pink, glabrous to villous abaxially, 4–5 cm long, 1.5–3 cm wide at base. Flowers 10 to 30 per cincinnus; pedicel white to pink, glabrous, 0.7–3 cm long; perianth white to light pink and glabrous basally, yellow and velutinous toward apex, 4.5–5.6 cm long, 1–1.2 cm wide at base, at anthesis curved 60–90° and sigmoid; free sepal reflexed, fused sepals with apices reflexed; staminode white (sometimes with yellow apex), 6–10 by 2–4 mm, apex acuminate to cuspidate; stamens with anthers connivent inside corolla apex; pollen *pogonantha* type, large (60–63 × 78–88 μm), euoblate ($P/E = 0.68\text{--}0.81$), heteropolar ($DR/PR = 5.79\text{--}8.7$) with the distal hemisphere convex, truncate, spinulose, the proximal hemisphere planar, psilate, the germination aperture distinct, flattened, sunken; ovary white to pale blue to lavender, glabrous, 7–10 by 5–7 mm. Drupes glabrous, 1.3–1.5 cm by 8–10 mm; pyrenes 9 by 5 mm.

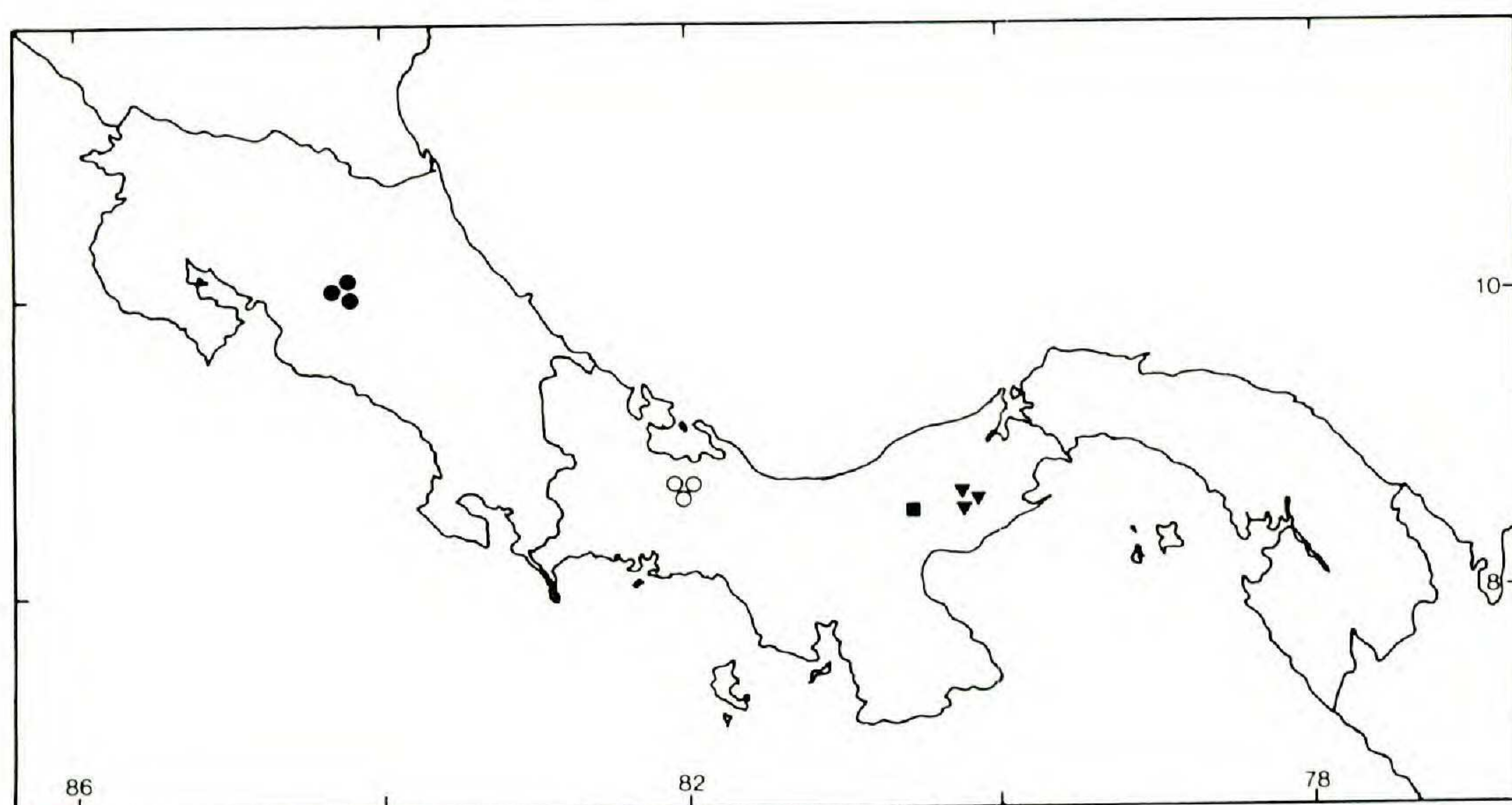
HABITAT AND DISTRIBUTION. *Heliconia ramonensis* occurs in middle-elevation (600–1200 m) forests of Costa Rica and Panama (MAP 10). Plants inhabit moist, forested slopes and often invade disturbed open areas.

VARIATION. The four varieties of *Heliconia ramonensis* are distinguished from each other by the distribution of the woolly vestiture on the peduncle, rachis, and cincinnal bracts, and by the color of the hairs on the floral bracts and perianth apices.

RELATIONSHIPS. *Heliconia ramonensis* belongs to the *pogonantha* group; it differs from other members of that group in the rusty orange hairs on various parts of its inflorescence and peduncle and in its bright pink to red cincinnal bracts.

Key to the Varieties of *Heliconia ramonensis*

- A. Peduncle, rachis, and cincinnal bracts all essentially glabrous. 16c. var. *glabra*.
- A. Peduncle, rachis, or cincinnal bracts villous to woolly.
 - B. Peduncle, rachis, and cincinnal bracts all woolly. 16d. var. *lanuginosa*.
 - B. Peduncle and sometimes rachis woolly, cincinnal bracts glabrous to villous.
 - C. Vestiture on floral bracts and perianth pale yellow to buff; cincinnal bracts red. 16a. var. *ramonensis*.
 - C. Vestiture on floral bracts and perianth bright yellow; cincinnal bracts rose-red to pink. 16b. var. *xanthotricha*.



MAP 10. Costa Rica and Panama, showing allopatric distribution of *Heliconia ramonensis* var. *ramonensis* (solid circles), var. *xanthotricha* (solid triangles), var. *glabra* (solid square), and var. *lanuginosa* (open circles).

16a. *Heliconia ramonensis* var. *ramonensis*

Herb to 5 m tall. Pseudostem 1.5–2 m tall, 4.5–6 cm in diameter; leaves with the petiole rusty green, 1.4–1.8 m long, 1.7–1.9 cm in diameter, the blade with base obtuse to truncate, the longest blade 1.6–2 m by 45–55 cm. Inflorescence to 85 cm long; peduncle red, woolly with golden hairs, 40–60 cm long, 1.8–2 cm in diameter; rachis red, villous to woolly with golden hairs, 1.5–2 cm in diameter at base; cincinnal bracts 20 to 30 per inflorescence, the middle bract with inner surface villous with golden hairs, outer surface red to pink-red and puberulous to scurfy, 9–10 cm long, 8–10 cm wide at base. Floral bracts pink, glabrous to villous with golden hairs abaxially, 4–5 cm long, 1.5–3 cm wide at base. Flowers 20 to 30 per cincinnus; pedicel 1.2–3 mm long; perianth glabrous basally, villous with golden hairs toward apex, 4.5–5.5 cm long, 1–1.2 cm wide at base; staminode white, yellow at apex, 7–10 by 3–4 mm; ovary pale lavender, 7–10 by 6–7 mm. Drupes not seen.

SPECIMENS EXAMINED. **Costa Rica.** ALAJUELA: Cataratas de San Ramón, Brenes 18370 (CR); 15 mi from San Ramón near La Balsa, elev. 1000 m, Kress *et al.* 76-604 (DUKE), 77-764 (DUKE); entre Balsa de San Ramón y Río Cataratas, ca. 12 km N of La Balsa, elev. 550–1100 m, Utley & Utley 3745 (DUKE).

PHENOLOGY. Flowering primarily during early rainy season (July to September); some inflorescences produced throughout year.

DISTRIBUTION. *Heliconia ramonensis* var. *ramonensis* is endemic to Costa Rica in the foothills (ca. 1000 m) above San Ramón (MAP 10).

- 16b. *Heliconia ramonensis* var. *xanthotricha* Kress, J. Arnold Arbor. **62**: 258. 1981. TYPE: Panama, Coclé, 6 mi beyond El Valle de Antón behind Cerro Gaital, elev. 900 m, Kress, Clarkson, & McDade 77-840 (holotype, DUKE!; isotypes, K!, MO!).

Heliconia vellerigera auct. non Poeppig: Woodson & Schery, Ann. Missouri Bot. Gard. 32: 55. 1945, in part (Woodson & Schery included *H. magnifica* and *H. ramonensis* in *H. vellerigera*).

Herb 4–5 m tall. Leafy shoots in groups of 3 to 10; pseudostem orange to brown, 1.3–2 m tall, 5–8 cm in diameter; leaves with the petiole green, 1–1.2 m long, 1.5–2 cm in diameter, the blade with base truncate to cordate, lower surface green tinted with maroon especially along margins, the longest blade 1.3–1.8 m by 40–60 cm wide. Inflorescence to 90 cm long; peduncle red, woolly with golden-yellow hairs, 30–50 cm long, 1.6–2 cm in diameter; rachis red-orange, velutinous to villous with yellow hairs, 1.5–2.2 cm in diameter at base; cincinnal bracts 20 to 40 per inflorescence, oriented 135–140° to axis of inflorescence, the middle bract with inner surface pink and velutinous to villous, outer surface rose-red, 9–12 cm long, 7–10 cm wide at base. Floral bracts white to pink, velutinous to villous with bright yellow hairs abaxially. Flowers 10 to 15 per cincinnus; pedicel 7–13 mm long; perianth glabrous basally, tomentose to velutinous with bright yellow hairs toward apex, especially along sepal margins, 5–6 cm long, 1–1.2 cm wide at base, at anthesis curved 90°; staminode 7–8 by 2–3 mm; ovary bluish white, 8–10 by 5–6 mm. Drupes 1.3–1.5 cm by 9–10 mm.

SPECIMENS EXAMINED. **Panama.** COCLÉ: base of three peaks beyond El Valle de Antón, elev. 800 m, *Kress & Cooper-Smith 76-651* (DUKE), *Kress & Hammel 83-1581* (DUKE), *Maas et al. 1725* (MO, U, US), elev. 800–1000 m, *Allen 1818* (MO), elev. 2500–3000 ft, *Lewis et al. 1750* (MO), *Luteyn & Kennedy 1718* (DUKE, MO); on trail to Las Minas, elev. 1000 m, *Allen 2707* (MO), *Allen 2867* (US); vic. Finca Tomas Arias, elev. 600 m, *Allen 3629* (US); foot of Cerro Pilón, elev. 2000 ft, *Porter et al. 4423* (scz, UC), *Croat 13471* (MO); La Mesa, 2.8–3.4 mi NW of El Valle de Antón, elev. 850–900 m, *Luteyn 4064* (DUKE), *Croat 25311* (MO), elev. 900 m, *Croat 14374* (MO, scz), *22952* (MO), *Antonio 1292* (MO), elev. 900 m, *Sullivan 541* (MO), *D'Arcy & Sytsma 14665* (MO); ca. 9 km from El Valle Market beyond Sr. Furlong's Finca, *Kennedy et al. 3223* (DUKE, MO); Cerro Gaital, N of El Valle, elev. 760 m, *Reveal & Balogh 4971* (MO), elev. 2200 ft, *Kress et al. 80-1161* (DUKE); near Cerro Turega, elev. 650–700 m, *Woodson & Schery 205* (MO); Cerro Caracoral, elev. 2700–3200 ft, *Sytsma 3764* (MO), *3799* (MO), *4053* (MO), *Andersson & Sytsma 1249* (s).

PHENOLOGY. Flowering mainly during rainy season (May to September); some inflorescences produced throughout year.

DISTRIBUTION. In Central America *Heliconia ramonensis* var. *xanthotricha* is found at middle elevations (650–1000 m) in Coclé, Panama, in the region around El Valle de Antón (MAP 10).

RELATIONSHIPS. Variety *xanthotricha* differs from vars. *ramonensis* and *lanuginosa* in the bright yellow vestiture on its floral bracts and perianth apices (also found in var. *glabra*), and in the contrasting colors of its red-orange rachis and rose-red cincinnal bracts.

16c. *Heliconia ramonensis* var. *glabra* Kress, var. nov.

A var. *ramonensi* inflorescentiis glabris et floribus pubescentiis luteis differt.

TYPE: Panama, Coclé, beyond sawmill above El Copé, elev. 2400 ft, *Kress & Hammel 83-1589* (holotype, DUKE!; isotype, MO!).

Herb 4–5 m tall. Leafy shoots in groups of 5 to 10; pseudostem green and brown, glabrous, 1–1.5 m tall, 5–7 cm in diameter; leaves with the petiole green, 1–1.2 m long, 1.1–1.5 cm in diameter, the blade with base cordate, apex acute, lower surface tinted maroon with maroon lateral venation and green midrib, the longest blade 1.1–1.3 m by 30–40 cm. Inflorescence to 50 cm long; peduncle rose-red, glabrous, 20–30 cm long, 1.3–1.5 cm in diameter; rachis rose-red, glabrous to scurfy, 1–1.3 cm in diameter at base; cincinnal bracts 20 to 30 per inflorescence, oriented 135° to axis of inflorescence, the middle bract with inner surface pink and velutinous with yellow hairs, outer surface rose-red to pink and glabrous, 7–8 cm long, 7–9 cm wide at base. Floral bracts white, villous with bright yellow hairs abaxially, 5 cm long, 2 cm wide at base. Flowers 25 per cincinnus; pedicel pink, 1 cm long; perianth with bright yellow hairs toward apex, 5.6 cm long, 1.2 cm wide at base, at anthesis curved 85°; staminode 6 by 2 mm; ovary white, 8 by 6 mm. Drupes not seen.

SPECIMENS EXAMINED. **Panama.** COCLÉ: area surrounding Rivera sawmill, 7 km N of El Copé, continental divide, elev. 750–860 m, *Folsom & Collins 6430* (DUKE, MO).

PHENOLOGY. Apparently flowering mainly during rainy season (July to November).

DISTRIBUTION. Although quite common at the type locality (pers. obs.), var. *glabra* has been collected only a few times and appears to be restricted to the mountains (750–850 m) above El Copé in Coclé, Panama (MAP 10).

RELATIONSHIPS. This variety is quite different from the other varieties of *Heliconia ramonensis* in its entirely glabrous peduncle, rachis, and cincinnal bracts. The bright yellow hairs of the floral bracts and perianths are also present in var. *xanthotricha*.

16d. ***Heliconia ramonensis* var. *lanuginosa*** Kress, var. nov. PLATE VII, B, D.

A var. *ramonensi* inflorescentiis omnibus lanuginosis et pubescentia ferruginea differt.

TYPE: Panama, Chiriquí, La Fortuna Dam site above Gualaca, elev. 3600 ft, *Kress & Hammel 83-1602* (holotype, DUKE!; isotypes, K!, MO!, PMA!).

Herb 5–6 m tall. Leafy shoots in groups of 2 to 5; pseudostem yellow to brown, glabrous to villous, 2 m tall, 5–6 cm in diameter; leaves with the petiole green and maroon, 1–1.2 m long, 1.6–1.8 cm in diameter, the blade with base truncate to cordate, lower surface green (sometimes with maroon borders), the longest blade 1.6–1.8 m by 37–44 cm. Inflorescence to 75 cm long; peduncle pink, woolly with rusty orange hairs, 20–50 cm long, 1.5–1.7 cm in diameter; rachis pink to pale yellow, woolly with rusty orange hairs, 1.4 cm in diameter at base; cincinnal bracts 20 to 25 per inflorescence, oriented 120–135° to axis of inflorescence, the middle bract with inner surface pale yellow and villous to velutinous with rusty orange hairs, outer surface pink to rose-red and villous to woolly with rusty orange hairs, 10–11 cm long, 7–9 cm wide at base. Floral bracts white, velutinous with rusty orange hairs abaxially, 4–4.5 cm long, 1.9–2 cm wide at base. Flowers 20 per cincinnus; pedicel white, 5–8 mm long;

perianth light pink basally, velutinous with rusty orange hairs apically, 5–5.5 cm long, 1.2 cm wide at base, at anthesis curved 90°; staminode white with yellow apex, 8–9 by 2 mm, apex acuminate; ovary white, 6–10 by 5 mm.

SPECIMENS EXAMINED. **Panama.** CHIRIQUÍ: along road between Gualaca and Fortuna Dam site, 7.9 mi NW of Los Planes de Hornito, elev. 1300 m, *Antonio 4130* (MO); N del sitio de presa de Fortuna, elev. 1000–1200 m, *Correa et al. 2317* (MO), *2670* (MO); Fortuna Dam site, elev. 1040 m, *Hammel 1989* (MO), elev. 1000–1200 m, *Kress et al. 82-1350* (DUKE), *Kress & Hammel 83-1600* (DUKE), elev. 1200–1400 m, *Folsom et al. 5493* (MO). BOCAS DEL TORO: Atlantic slopes beyond La Fortuna Dam site, elev. 1000 m, *Kress & Hammel 83-1604* (DUKE).

PHENOLOGY. Flowering mainly during rainy season (May to September).

DISTRIBUTION. Variety *lanuginosa* has been collected in the mountains (1000–1300 m) surrounding the Fortuna Hydroelectric Dam project in Chiriquí and neighboring Bocas del Toro, Panama (MAP 10).

RELATIONSHIPS. The inflorescences of this variety are conspicuously different from those of the other varieties in being entirely covered with a woolly indumentum of rusty orange hairs. In vars. *ramonensis* and *xanthotricha* this rusty vestiture is restricted mainly to the peduncle and rachis. The rusty orange hairs on the floral bracts and perianth of var. *lanuginosa* differ from the yellow hairs of the other varieties.

17. *Heliconia danielsiana* Kress, sp. nov. FIGURE 13; PLATE VIII, A, D.

Heliconia vellerigera auct. non Poeppig: Daniels & Stiles, *Brenesia* **15**(Supl.): 45. 1979.

Planta herbacea, 4.5–8 m alta; inflorescentia pendens, rubra, pubescentia lanata aurantiaca usque ad bubalinam; cincinnorum bracteae distichae vel subspirales; perianthium basi album apice lutescens, apice pubescentia cinnamomea usque ad bubalinum; ovarium album glabrum; fructus caeruleus glaber.

TYPE: Costa Rica, San José, 15 km above Dominical on road to San Isidro, elev. 2800 ft, *Kress & Clarkson 79-1097* (holotype, DUKE!; isotypes, CR!, F!).

Herb with *Musa*-like habit, 4.5–8 m tall. Leafy shoots in groups of 5 to 15; pseudostem brown, scurfy to villous, 1.8–3 m tall, 5–8 cm in diameter; leaves 2 to 4 per shoot; petiole green to yellow, glabrous, 1–1.8 m long, 2–2.5 cm in diameter; blade with the base unequal, truncate to cordate, the apex acute, the upper surface green to dark green, glabrous, with midrib green to yellow and glabrous, the lower surface green, slightly glaucous, midrib green to yellow with maroon midstripe and glabrous, the longest blade 2–2.8 m by 45–57 cm. Inflorescence pendent, to 1 m long; peduncle orange to red, woolly with orange (when fresh) to buff (when dried) hairs, 10–40 cm long, 1.6–2 cm in diameter; rachis flexuose, orange to red, woolly, 1.6–2 cm in diameter at base; cincinnal bracts distichous to subspirally arranged, 20 to 30 per inflorescence, oriented 130–150° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex acute to acuminate, margins straight to involute, inner surface pink and velutinous, outer surface orange-red and woolly with orange (when

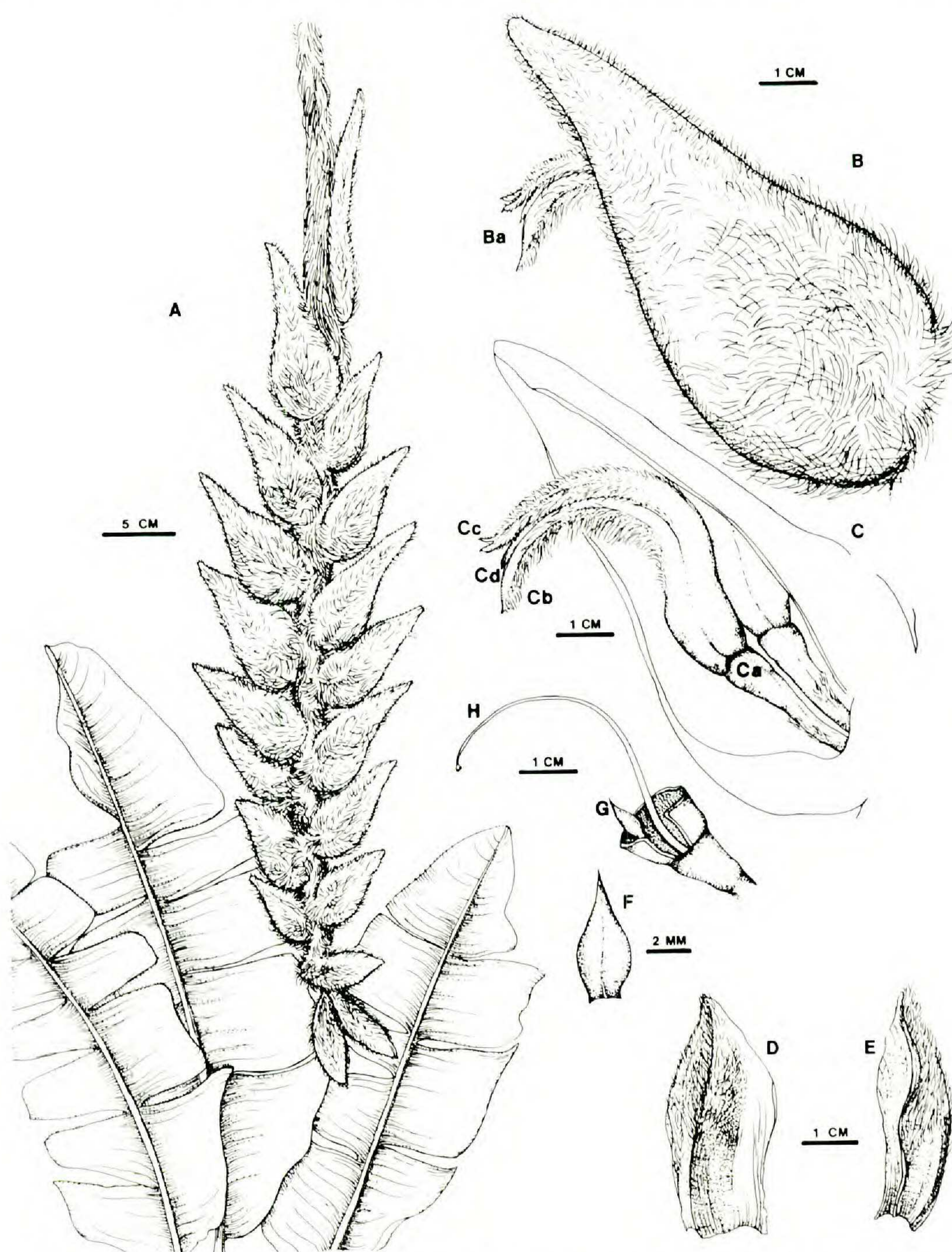
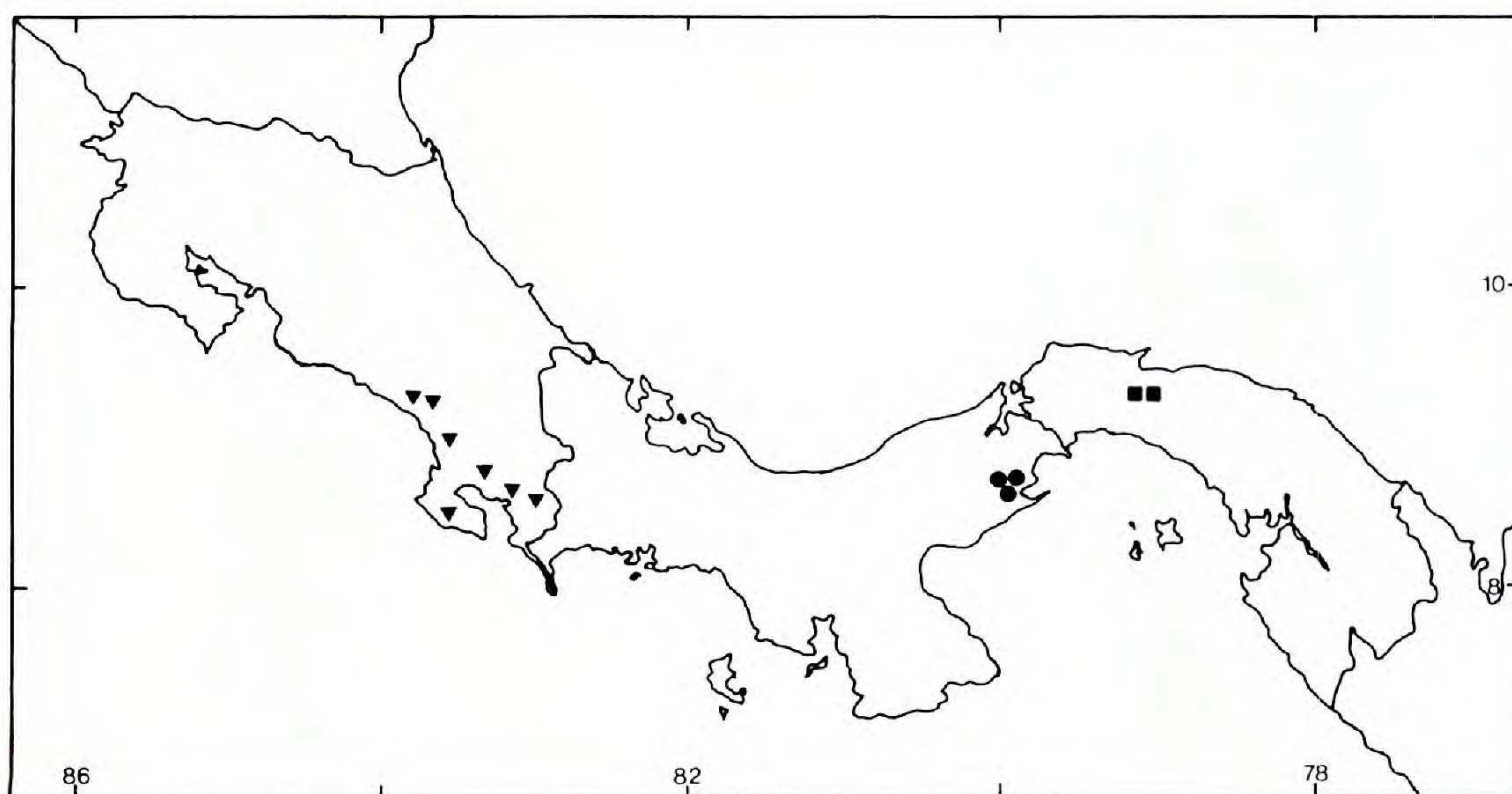


FIGURE 13. *Heliconia danielsiana*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, slightly reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, G, staminode: F, abaxial view; G, position relative to style, lateral view. H, style and stigma.

fresh) to buff (when dried) hairs, 9.5–11 cm long, 8–10 cm wide at base, l/w = 1.1. Floral bracts opaque, persistent, white to pink, velutinous to villous with golden hairs abaxially, 4–5 cm long, 2–2.5 cm wide at base. Flowers 15 to 20 per cincinnus; pedicel white to pink, glabrous to puberulous, 9–12 mm long; perianth white and glabrous basally, yellow and velutinous with cinnamon to



MAP 11. Costa Rica and Panama, showing allopatric distribution of *Heliconia danielsiana* (triangles), *H. magnifica* (circles), and *H. xanthovillosa* (squares).

buff hairs apically, 5.1–5.7 cm long, 1–1.2 cm wide at base, at anthesis curved 85–90° and sigmoid; free sepal slightly reflexed, fused sepals with apices slightly reflexed; staminode white with yellow apex, 5–7 by 2–3 mm, apex acuminate; stamens with anthers connivent inside perianth apex; pollen *pogonantha* type, large ($60 \times 86 \mu\text{m}$), euoblate ($P/E = 0.71$), heteropolar ($DR/PR = 7.9$) with the distal hemisphere convex, truncate, spinulose, the proximal hemisphere planar, psilate, the germination pore distinct, flattened, sunken; ovary white, glabrous, 8–10 by 5–6 mm. Drupes glabrous.

SPECIMENS EXAMINED. **Costa Rica.** PUNTARENAS: Golfo Dulce area, vic. Esquinas Experiment Station, sea level, *Allen 5235* (US); entre Los Ríos Piedras Blancas y Esquinas, Osa, elev. 75 m, *Jiménez 2248* (F, GH, NY); Esquinas Forest Reserve between Palmar and Río Claro, elev. ca. 100 ft, *Kress et al. 76-589* (DUKE), *Kress 78-1046* (DUKE); forest 30 km SE of Palmar Sur on Pan Am Hwy., *Lent 171* (CR); forest of Río Convento, 36 km S of San Isidro del General, elev. 500 m, *Molina et al. 17980* (NY); 8 mi from Villa Neily on road to San Vito, elev. 3500 ft, *Kress et al. 77-821* (DUKE); San Vito de Java, cult. at Las Cruces Trop. Bot. Garden, elev. ca. 4000 ft, *Kress 76-575* (DUKE), *78-1031* (DUKE); Golfito, along trail to TV tower, steep forested slopes, elev. 100–300 m, *Burger & Matta 4772* (CR), *4773* (CR, F, GH, US); Península de Osa, Corcovado Natl. Park, elev. 20–400 m, *Liesner 3177* (MO); Península de Osa, Camino de Altura, 2–5 mi W of Rincón de Osa, elev. 400–1000 ft, *Raven 21494* (CR, F). SAN JOSÉ: El General Valley, vic. of San Isidro del General, elev. 500 m, *Molina et al. 17980* (F); between San Isidro and Playa Dominical, *Sheffy 62* (CR).

PHENOLOGY. Flowering throughout year, with slight peak in early rainy season (June to August).

HABITAT AND DISTRIBUTION. *Heliconia danielsiana* is restricted to Costa Rica, where it occurs only on the Pacific slopes from Dominical to the Golfo Dulce area (MAP 11). This species inhabits open disturbed areas from sea level to 1200 m.

RELATIONSHIPS. This species, a member of the *pogonantha* group, has extremely woolly inflorescences. It is distinguished by its orange-red cincinnal bracts and by the orange to buff vestiture densely covering the entire inflorescence.

NOMENCLATURE. Daniels and Stiles (1979) applied the name *Heliconia vellerigera* Poeppig to the Costa Rican species characterized by an extremely woolly vestiture covering the entire pendent inflorescence. Indeed, Poeppig had described such a plant from Peru and deposited a type at Vienna (w). The type specimen is minimal, consisting only of several cincinnal bracts, and does not have any flowers or leaves. Other collections seen from Peru (e.g., *Ferreya* 1198, US; *Berlin* 383, F; *Plowman & Schunke* 11471, DUKE, F) and Colombia (*Foster & Foster* 2270, GH) with similar woolly inflorescences have glabrous flowers that differ from the velutinous flowers of plants found in Costa Rica. The large geographic distance between the type locality of *H. vellerigera* and Costa Rica and the difference in the vestiture of the flowers leave no doubt that the plants found in Costa Rica are specifically distinct from Poeppig's taxon. The specific epithet proposed here honors Dr. Gilbert S. Daniels, who has contributed much to our understanding of the *Heliconia* taxa of Costa Rica, and who first showed me the new species in its native habitat.

18. ***Heliconia magnifica*** Kress, J. Arnold Arbor. **62**: 246. 1981. TYPE: Panama, Panamá, Cerro Campana, beyond Su Lin Motel, elev. 1000 m, *Kress, Clarkson, & McDade* 77-850 (holotype, DUKE!; isotypes, K!, MO!).

FIGURE 14; PLATE VIII, B, E.

Heliconia vellerigera auct. non Poeppig: Woodson & Schery, Ann. Missouri Bot. Gard. **32**: 54. 1945, in part (Woodson & Schery included *H. magnifica* and *H. ramonensis* var. *xanthotricha* in *H. vellerigera*).

Herb with *Musa*-like habit, 4–6 m tall. Leafy shoots solitary or in groups of 2 to 5; pseudostem rusty brown, scurfy to villous, 1.1–2.3 m tall, 3–7 cm in diameter; leaves 3 or 4 per shoot; longest petiole light green and maroon, glabrous, 1.1–1.8 m long, 1–1.9 cm in diameter; blades splitting into narrow lateral segments with age, the base unequal, truncate to cordate, the apex acute, the upper surface dark green, glabrous, with midrib yellow-green and glabrous, the lower surface green with maroon margins, glabrous, with midrib yellow-green and glabrous, the longest blade 1.1–1.9 m by 36–55 cm. Inflorescence pendent, to 94 cm long; peduncle dark red to burgundy, woolly with golden to burgundy hairs, 30–50 cm long, 1–1.7 cm in diameter; rachis flexuose, twisted, red to burgundy, woolly, 1–1.6 cm in diameter at base; cincinnal bracts spirally arranged, up to 35 per inflorescence, oriented 130–150° to axis of inflorescence, the basal bract usually fertile, the middle bract with apex acuminate, margins straight becoming involute at base, inner surface white to red and pubescent to velutinous, outer surface red to burgundy and villous to woolly with burgundy hairs, 8–10 cm long, 7.5–9.5 cm wide at base, l/w = 1.1. Floral bracts opaque, persistent, pink, velutinous abaxially, 3.5–5 cm long, 1–1.5 cm wide at base. Flowers 10 to 15 per cincinnus; pedicel white, pink near ovary, glabrous, 1–1.3 cm long; perianth white and glabrous basally, yellow and velutinous with

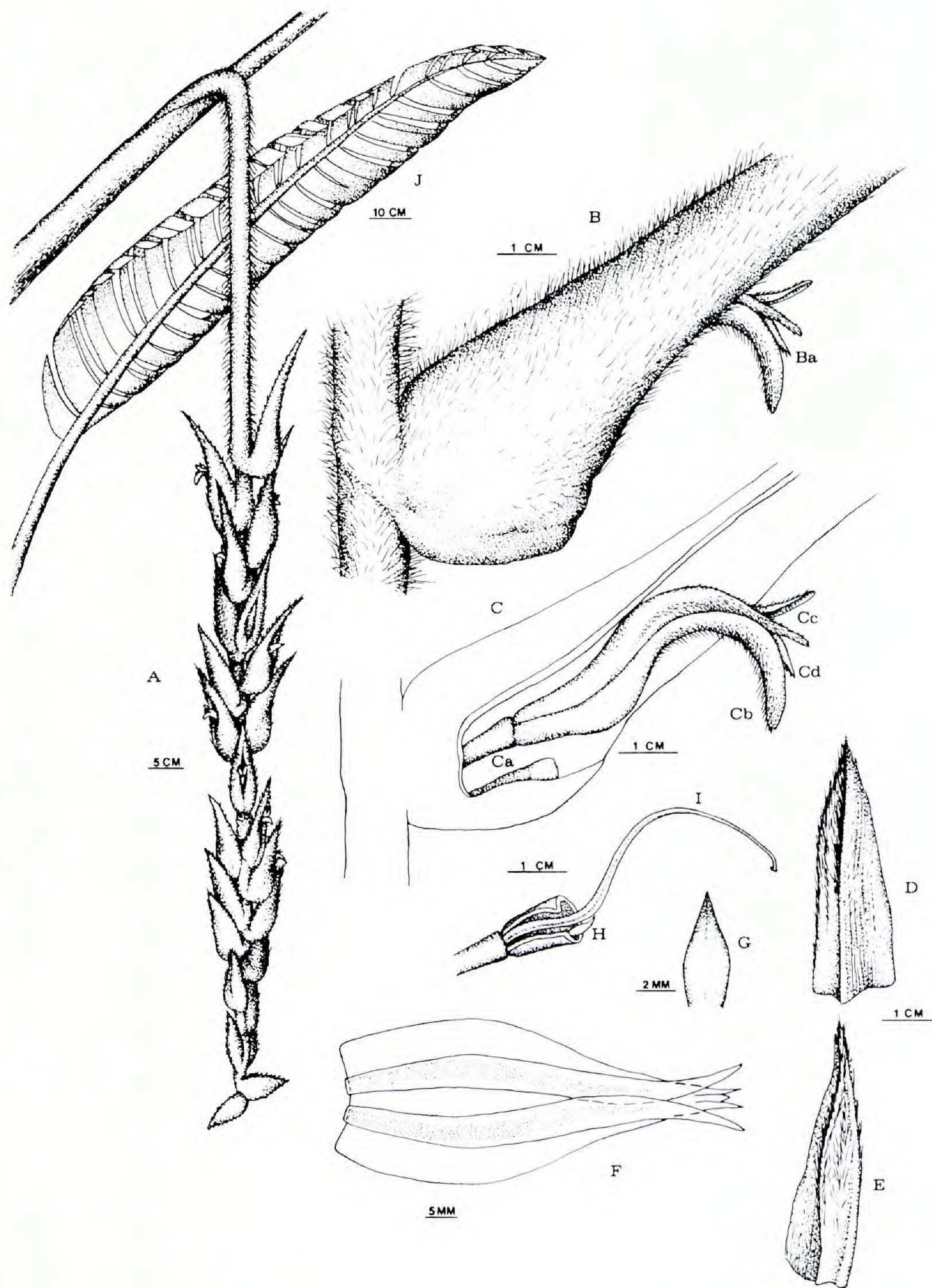


FIGURE 14. *Heliconia magnifica*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, partially reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma. J, mature leaf, blade split into lateral segments.

golden hairs toward apex, 5.5–6 cm long, 1–1.2 cm wide at base, at anthesis curved 80–90° and sigmoid; free sepal reflexed, fused sepals with apices slightly reflexed; staminode white, yellow at apex, 5–6 by 2–3 mm, apex acuminate; stamens with anthers connivent inside apex of corolla tube; pollen *pogonantha* type, large ($65 \times 82 \mu\text{m}$), suboblate ($P/E = 0.78$), heteropolar ($DR/PR = 6.07$) with the distal hemisphere convex, truncate, spinulose, the proximal hemisphere planar, psilate, the germination aperture distinct, flattened, sunken; ovary white, glabrous, 1–1.1 cm by 5–6 mm. Drupes glabrous, 1.2–1.3 cm by 8–10 mm; pyrenes 9 by 6 mm.

SPECIMENS EXAMINED. **Panama.** PANAMÁ: Cerro Campana, elev. 600 m, *Antonio* 1250 (MO), 1725 (MO), 4855 (MO), elev. 700–800 m, *Andersson* 1317 (GB, s), elev. 850 m, *Busey* 847 (MO), *Liesner* 627 (F, MO, NY), elev. 875 m, *Croat* 25239 (MO), elev. 2600–2800 ft, *Lewis et al.* 1903 (MO), elev. 800–1000 m, *Gentry* 4955 (F, MO, SCZ), elev. 1000 m, *Allen* 2425 (MO, s), near summit, elev. 1000 m, *Kress & Cooper-Smith* 76-648 (DUKE), elev. 2800 ft, *Sytsma* 1233 (MO), elev. 2700–3200 ft, *Hammel* 3783 (MO), elev. 3300 ft, *Kress* 80-1246 (DUKE), $\frac{3}{4}$ of way to summit from Pan American Hwy., *Dwyer et al.* 4850 (MO), cloud forest, *Luteyn & Kennedy* 1814 (DUKE), without further location, *C. E. Smith & H. M. Smith* 3399 (US).

PHENOLOGY. Flowering mainly March to September; some mature inflorescences all year.

HABITAT AND DISTRIBUTION. This species is found at middle elevations in the understory of cloud forest. It is endemic to Cerro Campana in Panama at elevations above 600 m (MAP 11).

RELATIONSHIPS. *Heliconia magnifica* is closely related to other species of the *pogonantha* group with large pendent woolly inflorescences, including *H. danielsiana*, *H. ramonensis*, and *H. xanthovillosa*, found in Central America. It is distinguished from these species by the dark red to burgundy color of its inflorescence and the red to golden woolly pubescence covering its peduncle, rachis, and cincinnal bracts.

19. ***Heliconia xanthovillosa*** Kress, J. Arnold Arbor. **62**: 253. [21 Aug.] 1981.

TYPE: Panama, Panamá, El Llano–Cartí Road, 12 km from intersection with Pan American Hwy., elev. 500 m, *Kress & Knapp* 80-1233 (holotype, DUKE!; isotypes, F!, GH!, K!, MO!, PMA!).

FIGURE 15; PLATE VIII, C, F.

Heliconia dresslerana Abalo & Antonio, *Baileya* **21**: 139. [17 Sept.] 1981. TYPE: Panama, Panamá, El Llano–Cartí Road, 15 km N of Panamerican Hwy. at El Llano, *Antonio* 5258 (holotype, MO!; isotypes, PMA, US).

Herb with *Musa*-like habit, 3.5–4.5(–7) m tall. Leafy shoots in groups of 2 to 11; pseudostem brown, scurfy to puberulous, 1.6–1.9(–3.5) m tall, 6–7 cm in diameter; leaves 4 per shoot; petiole dull green, glabrous, 1.1–1.2 m long, 1.9–2(–2.5) cm in diameter; blade with the base unequal, obtuse to truncate, the apex acute, the upper surface green to dark green, glabrous, with midrib light green and glabrous, the lower surface green, glabrous, with midrib yellow-green and glabrous, the longest blade 1.9–2.3 m by 49–55 cm. Inflorescence

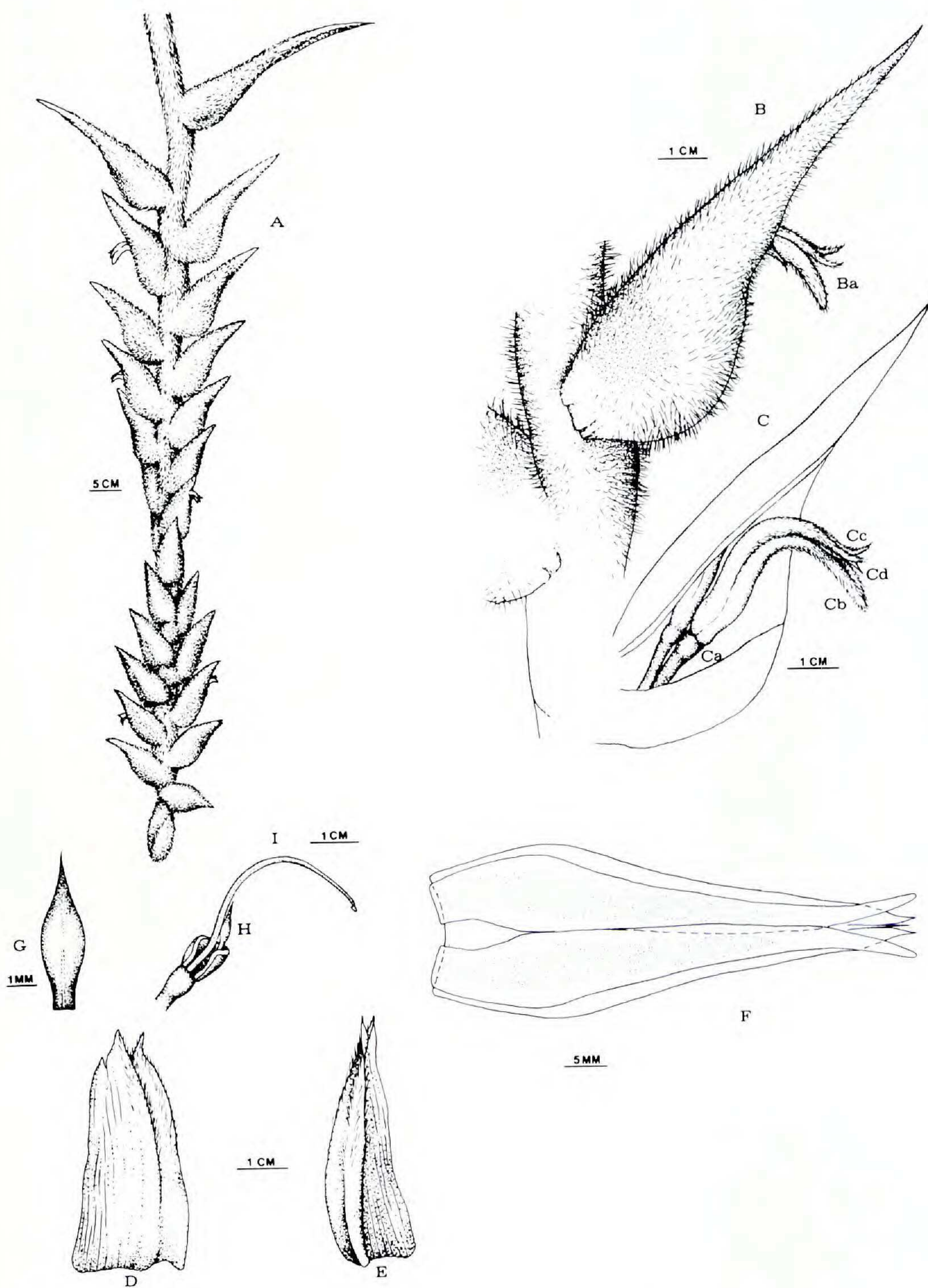


FIGURE 15. *Heliconia xanthovillosa*. A, inflorescence. B, C, cincinnal bracts: B, entire (Ba, flower protruding at anthesis); C, cut-away, floral bracts removed showing flower at anthesis (Ca, ovary; Cb, free sepal; Cc, fused sepals, slightly reflexed; Cd, anthers, included in apex of corolla tube). D, E, floral bracts: D, abaxial view; E, lateral view. F, perianth, outer surface showing 2 sepals fused to partially spread-open corolla tube. G, H, staminode: G, abaxial view; H, position relative to style, lateral view. I, style and stigma.

pendent, to 86(–105) cm long; peduncle bright yellow-green, woolly with yellow hairs, 26–68 cm long, 1.5–2.2 cm in diameter; rachis flexuose, bright yellow, woolly with yellow hairs, 1.5–1.9 cm in diameter at base; cincinnal bracts distichous to subspirally arranged, up to 35 per inflorescence, oriented 135–145° to axis of inflorescence, the basal bract sterile or fertile, the middle bract with apex acuminate to acute, margins straight to involute at base, inner surface pale yellow-green (sometimes pink) and villous, outer surface bright yellow to green-yellow (sometimes red distally) and woolly with yellow hairs, 8–10 cm long, 7–8 cm wide at base, $l/w = 1.2$. Floral bracts opaque, persistent through fruiting, pale yellow, velutinous to villous abaxially, 3.7–4.8 cm long, 1.6–1.7 cm wide at base. Flowers 12 to 20 per cincinnus; pedicel white, glabrous (to hirsute with yellow hairs), 1 cm long; perianth white and glabrous basally, yellow and velutinous to villous with bright yellow hairs distally, 5.1–5.5 cm long, 9–11 mm wide at base, at anthesis curved 85–90° and sigmoid; free sepal reflexed, fused sepals with apices slightly reflexed; staminode white, 5(–8) by 3(–5) mm, apex acuminate; stamens with anthers connivent inside apex of corolla tube; pollen *pogonantha* type, large ($65 \times 81 \mu\text{m}$), suboblate ($P/E = 0.79$), heteropolar ($DR/PR = 6.63$), with the distal hemisphere convex, truncate, spinulose, the proximal hemisphere planar, psilate, the germination aperture distinct, flattened, sunken; ovary white, glabrous, 7–8 by 5–6 mm. Drupes glabrous, 1.1–1.2 cm by 8 mm; pyrenes 8–9 by 5–6 mm.

SPECIMENS EXAMINED. **Panama.** PANAMÁ: El Llano–Cartí Road, 8 mi from Pan American Hwy., elev. 1200 ft, *Antonio 1699* (MO), elev. 300–500 m, *Folsom & Maas 5214* (MO), *Antonio 1266* (MO), *1277* (MO), *Folsom 3507* (MO), *Maas et al. 2810* (GB), *Andersson & Sytsma 1262* (GB, s), *Knapp et al. 4747* (MO), *Kress & Hammel 82-1335* (DUKE), *83-1564* (DUKE), *83-1565* (DUKE), *Kress & Knapp 80-1235* (DUKE).

PHENOLOGY. Flowering during rainy season (May to October); fruiting probably well into November.

HABITAT AND DISTRIBUTION. This species is found at middle elevations (300–500 m) in open areas in the forest, and now especially in areas disturbed by man. It has been collected only along the continental divide separating the drier Pacific slopes from the wetter Atlantic ones in eastern Panama above the Río Cartí (MAP 11).

VARIATION. Several individuals having large, stout inflorescences with yellow and red cincinnal bracts (*Antonio 1277*; *Kress & Knapp 83-1235*; *Kress & Hammel 82-1335*, *83-1564*) have been collected on El Llano–Cartí Road. Although differing in bract color, the inflorescences are covered with the same yellow vestiture as typical *Heliconia xanthovillosa* and are thus considered a color form of that species.

RELATIONSHIPS. *Heliconia xanthovillosa* is closely related to species of the *pogonantha* group, especially *H. danielsiana*, *H. ramonensis*, and *H. magnifica*, which differ from each other essentially in cincinnal-bract and indumentum color. *Heliconia xanthovillosa* has bright yellow inflorescences that are entirely covered with long, yellow hairs.

INSUFFICIENTLY KNOWN TAXON

In the examination of numerous herbarium specimens, several collections from Panama (one from the Burica Peninsula in Chiriquí and two from Darién) have proved quite difficult to assign to any of the taxa of *Heliconia* with pendent inflorescences included here. These specimens have a characteristic inflorescence with a strongly flexuose rachis and nearly overlapping cincinnal bracts. The cincinnal bracts are distinctive in having apparently necrotic apices that are either black or green (due to algal growth?). Dodson and Gentry (1978) have described a species from Ecuador, *H. nigripraefixa*, that has the same feature. I do not think that these specimens should be placed in that taxon until further comparative studies can be made on living specimens in the field.

SPECIMENS EXAMINED. **Panama.** CHIRIQUÍ: Península de Burica, 20 km W of Puerto Armuelles, elev. 400–600 m, *Busey 551* (MO). DARIÉN: headwater of Río Tuquesa, ca. 2 km from continental divide, vicinity gold-mining camp of Tyler Kittredge, *Croat 27140* (MO), *27141* (MO).

NATURAL HYBRIDS

Natural hybrids are rare in *Heliconia*. As discussed earlier, attempts to artificially hybridize a wide range of heliconias have proved unsuccessful. Strong physiological stigma/style barriers to foreign pollen penetration are present in most species (Kress, 1981b, 1983b). Although a limited number of hybrids have been found involving species with pendent inflorescences (TABLE 7), only two—*H. curtispatha* × *H. pogonantha* var. *holerythra* and *H. mariae* × *H. pogonantha* var. *holerythra*—are known to occur in more than one locality. Detailed morphological descriptions and comparisons of the three parent taxa and their two hybrid offspring are given in TABLE 8.

The hybrid nature of the plants listed in TABLE 7 (excluding those cited by

TABLE 7. Natural hybrids of *Heliconia* involving species with pendent inflorescences.

HYBRID COMBINATION	COUNTRY	VOUCHER NUMBER* OR LITERATURE CITATION
<i>H. curtispatha</i> × <i>H. pogonantha</i>	Panama	<i>Kress 80-1144, 80-1156</i>
<i>H. mariae</i> × <i>H. pogonantha</i>	Costa Rica	<i>Kress 76-627, 76-659, 77-795, 77-875</i> <i>Williams 686</i>
<i>H. nutans</i> × <i>H. lankesteri</i>	Panama	<i>Kress & Clarkson 79-1089c</i>
<i>H. secunda</i> × <i>H. clinophila</i>	Costa Rica	<i>Kress 77-777</i>
<i>H. stilesii</i> × <i>H. danielsiana</i>	Costa Rica	Daniels & Stiles (1979)
<i>H. tortuosa</i> × <i>H. nutans</i>	Costa Rica	Daniels & Stiles (1979)

*For collection localities and herbaria, see “Specimens Examined” under each hybrid in text.

TABLE 8. Morphological comparison of *Heliconia curtispatha*, *H. pogonantha* var. *holerythra*, *H. mariae*, and their putative hybrids.

CHARACTER	H. CURTISPATHA	"HYBRID"	H. POGONANTHA VAR. HOLERYTHRA	"HYBRID"	H. MARIAE
Height (m)	6–7	7–8	4.5–7.5	6	4–7.5
Petiole					
Length (m)	0.9–1.5	1.7–2	1.1–1.8	1.2–1.4	0.9–1.7
Diameter (cm)	1.5–2.3	2.2	2–3	2.2–2.6	1.5–2.5
Leafblade					
Lower surface	Glaucous	Glaucous	Slightly glaucous	Glabrous	Glabrous
Length (m)	1.9–2.3	2.8–3	2–3.3	2.3–2.7	1.7–2.5
Width (cm)	35–55	50–60	40–65	50–60	45–65
Peduncle vestiture	Absent to scurfy	Scurfy	Scurfy	Scurfy	Densely scurfy
Inflorescence length (excluding peduncle) (m)	1.6	1.5	1.6	1	0.65
Rachis					
Vestiture	Puberulous to scurfy	Puberulous to scurfy	Scurfy	Scurfy	Absent to scurfy
Diameter (cm)	1.2–1.8	2	2–2.5	1.8–2.2	1.5–1.8
Cincinnal bracts					
Arrangement	Distichous to spiral	Spiral	Spiral	Distichous to spiral	Distichous
Orientation (to inflorescence axis)	35–50°	50–60°	40–60°	40–50°	80–90°
Inner surface color	Yellow-orange to pink	Yellow to red	Yellow-red	White to yellow to pink	White to pink
Inner surface vestiture	Tomentose to velutinous	Puberulous to pubescent	Puberulous	Absent to puberulous	Absent
Outer surface color	Red to yellow-orange	Rose-red	Red	Red	Pink to red
Outer surface vestiture	Puberulous	Absent	Puberulous	Puberulous to scurfy	Absent to scurfy

Length (cm)	8.5–11.5	12–15	10–13	6–11	4.5–6.5
Width (cm)	6.5–9	7–9	11–16	8–12	7.5–9
Floral bract vestiture (abaxially)	Velutinous to villous	Pubescent	Absent to velutinous	Absent to villous	Absent to puberulous
Pedicel					
Color	White to yellow	White to pink	White to pink	White	White to pink
Vestiture	Absent to puberulous	Absent to puberulous	Absent	Absent to puberulous	Absent to puberulous
Perianth					
Color (base/apex)	White to yellow/deep yellow	Pink/yellow	White to pink/yellow	White/yellow suffused with pink	White/pink to red
Vestiture	Absent, to slightly puberulous apically	Absent to puberulous	Absent basally, velutinous apically	Absent basally, pubescent apically and along sepal margins	Absent basally, puberulous apically
Length (cm)	5.5–6.5	4.6–6	5–5.7	4–5	3–4
Curvature, shape	70–90°, parabolic	90°, parabolic	75–85°, sigmoid	70°, parabolic	50–70°, parabolic
Staminode					
Color	White	White	White, yellow at apex	White, yellow at apex	White
Apex	Cuspidate	Cuspidate	Acuminate	Acuminate	Acute to acuminate
Length (mm)	6–8	7	6–8	5–6	5–7
Drupe					
Length (cm)	1.7	(no fruits seen)	1.5–2	1.3–1.5	1–1.2
Width (cm)	1	(no fruits seen)	1–1.3	0.9–1	0.7–0.9
Flowering	Throughout year	January to August	January to August	(January? to) August	Throughout year
Habitat	Old secondary and primary forest	Open secondary growth	Open secondary growth	Open secondary growth	Open secondary growth

1984]

KRESS, HELICONIA

Daniels and Stiles, 1979) was evaluated according to several criteria. In all cases the hybrid individual was intermediate in many of the parental morphological characters (see TABLE 8) and was easily distinguished in the field from both parents, which were always growing in the immediate vicinity. Except for *Heliconia nutans* × *H. lankesteri*, hybrids were usually found in areas of recent disturbance, indicating possible breakdown of habitat- and pollinator-isolating mechanisms. Hybrid pollen grains appeared distorted and highly variable in size under the scanning electron microscope (Kress & Stone, 1983), and they germinated poorly in sucrose solutions. Natural hybrids of *Heliconia* rarely produce viable seed (Stiles, 1979; pers. obs.). However, in the most common hybrid, *H. mariae* × *H. pogonantha*, mature fruits containing fully formed seeds have been found. In no case, except possibly in *H. nutans* × *H. lankesteri*, was any type of "hybrid swarm" apparent; all hybrids occurred as a single individual plant.

***Heliconia curtispatha* Peterson × *H. pogonantha* var. *holerythra* Daniels & Stiles**

SPECIMENS EXAMINED. **Panama.** COLÓN: along Río Guanche, elev. ca. 100 ft, *Kress et al.* 80-1156 (DUKE). PANAMÁ: El Llano–Cartí Rd., 15 km from Pan Am Hwy. turnoff, elev. 1200 ft, *Kress & Hammel* 80-1144 (DUKE).

***Heliconia mariae* J. D. Hooker × *H. pogonantha* var. *holerythra* Daniels & Stiles**

SPECIMENS EXAMINED. **Costa Rica.** LIMÓN: along road between Puerto Viejo and BriBrí, elev. ca. 100 m, *Kress et al.* 76-627 (DUKE), *Kress* 77-795 (DUKE). **Panama.** COLÓN: along Río Guanche, elev. 25 m, *Kress* 76-659 (DUKE); along roadside near Río Buenaventura, 3 mi from Portobelo, ca. sea level, *Kress* 77-875 (DUKE). DARIÉN: Marraganti and vic., elev. 10–200 ft, *Williams* 686 (NY).

***Heliconia nutans* Woodson × *H. lankesteri* var. *rubra* Daniels & Stiles**

SPECIMEN EXAMINED. **Panama.** CHIRIQUÍ: in forest along Río Chiriquí Viejo below Cerro Punta, elev. 5500 ft, *Kress & Clarkson* 79-1089c (DUKE).

***Heliconia secunda* R. R. Smith var. *secunda* × *H. clinophila* R. R. Smith**

SPECIMEN EXAMINED. **Costa Rica.** HEREDIA: near waterfall at Cinchona, elev. 4400 ft, *Kress* 77-777 (DUKE).

***Heliconia stilesii* Kress × *H. danielsiana* Kress**

Reported by Daniels and Stiles (1979) to occur around Golfito, Puntarenas, Costa Rica. No specimens cited.

***Heliconia tortuosa* Griggs × *H. nutans* Woodson**

Reported by Daniels and Stiles (1979) to occur at Las Alturas, Puntarenas, Costa Rica. No specimens cited.

ACKNOWLEDGMENTS

Many friends and colleagues have given freely of their time and advice during the preparation of this revision, and my thanks go to all.

Dr. Timothy Plowman first suggested *Heliconia* as a possible genus in need of revision, and these pages are dedicated to him. Dr. Lindsay Clarkson's unfading and unfailing moral and intellectual encouragement were indispensable to the completion of this work. Dr. Lennart Andersson has proved a venerable friend and critic during our lengthy debates about *Heliconia*. I look forward to our continued exchange of ideas.

Drs. L. Andersson, J. Lundberg, D. Stone, R. White, R. Wilbur, and P. Stevens critically read and advised on various sections of the manuscript. I have had numerous discussions with Drs. F. G. Stiles, G. Daniels, L. Andersson, R. Wilbur, and D. Stone on the biology and taxonomy of *Heliconia*. Drs. C. Humphries, J. Lundberg, and L. McDade convinced me of the significance and importance of phylogenetic systematics. B. Hammel, L. McDade, J. Cooper-Smith, and S. Knapp helped with collections and in all kinds of weather endured my lengthy field notations. J. MacDougal, M. Turner, and B. Kirchoff helped solve problems seemingly small to them but important to me. W. L. Culberson shared his expertise in botanical Latin. S. Sellers, L. Eibest, and P. Atkins provided endless technical assistance in electron microscopy, manuscript preparation, and greenhouse care, respectively. S. Dickerson and J. Daniels typed the manuscript. During my stay in Costa Rica, Ms. Flor Torres and her staff at the Organization for Tropical Studies provided invaluable logistic support; at the Las Cruces Tropical Botanical Garden Robert and Katherine Wilson helped in numerous ways.

I thank S. Schrohenloher, C. Taylor, and S. K. Hamilton for their artistic skill and botanical eye in the preparation of the illustrations.

The expert and meticulous editorial assistance of E. Schmidt and S. Sponberg was invaluable and enlightening.

Financial assistance was provided by a Duke University Graduate School Research Award to W. J. Kress, by Biomedical Research Support Grant No. 303-3806 to D. E. Stone, and by Mr. Rob Montgomery, of Nahiku, Hawaii. The Stanley Smith Horticultural Trust provided funds in part for the publication of the color plates.

This material is also based upon research supported by the National Science Foundation (Grants DEB-7701556, DEB-7724612, and BSR-8306939) and is published with support of National Science Foundation Grant BSR-8317553. The Foundation provides awards for research and education in the sciences. The awardee is wholly responsible for the conduct of such research and preparation of the results for publication. The Foundation, therefore, does not assume responsibility for such findings or their interpretation. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author and do not necessarily reflect the view of the National Science Foundation.

LITERATURE CITED

- ABALO, J. E., & L. G. MORALES. 1982. Veinticinco (25) heliconias nuevas de Colombia. *Phytologia* **51**: 1–61.
- & ———. 1983a. Doce (12) heliconias nuevas del Ecuador. *Ibid.* **52**: 387–413.
- & ———. 1983b. Diez (10) heliconias nuevas de Colombia. *Ibid.* **54**: 411–433.
- ADANSON, M. 1763. *Gingembres. Zingiberes. Familles des plantes*. Vol. 2. Pp. 61–67. Vincent, Paris.
- ANDERSSON, L. 1981. Revision of *Heliconia* sect. *Heliconia* (Musaceae). *Nordic J. Bot.* **1**: 759–784.
- ARGENT, G. C. G. 1976. The wild bananas of Papua New Guinea. *Notes Roy. Bot. Gard. Edinburgh* **35**: 77–114.
- ARISTEGUIETA, L. 1961. El género *Heliconia* in Venezuela. Instituto Botánico, Caracas.
- ARNOLD, E. N. 1981. Estimating phylogenies at low taxonomic levels. *Z. Zool. Syst. Evolut.-forsch.* **19**: 1–35.
- BAKER, J. G. 1893. A synopsis of the genera and species of Museae. *Ann. Bot. (London)* **7**: 189–222.
- BARREIROS, H. S. 1971. Una nova especie de *Heliconia* L. (Musaceae) de le raque pendula. *Rodriguésia* **23**: 127–130.
- . 1976. *Heliconiae novae Americanae* (Heliconiaceae). *Ibid.* **28**: 129–132.
- . 1978. *Heliconia bahiensis* Barreiros n. sp. (Heliconiaceae). *Ibid.* **29**: 225–227.
- BELL, A. D., & P. B. TOMLINSON. 1980. Adaptive architecture in rhizomatous plants. *J. Linn. Soc., Bot.* **80**: 125–160.
- BENTHAM, G., & J. D. HOOKER. 1880. *Genera plantarum*. Vol. 3. L. Reeve & Co.; Williams & Norgate, London.
- BISSON, S., S. GUILLEMET, J.-L. HAMEL. 1968. Contribution à l'étude caryo-taxinomique des Scitaminées. *Mém. Mus. Natl. Hist. Nat., Sér. B, Bot.* **18**: 59–146.
- BREMER, K., & H.-E. WANNTORP. 1978. Phylogenetic systematics in botany. *Taxon* **27**: 317–329.
- COOMBS, E. A. K., M. J. DONOGHUE, & R. J. MCGINLEY. 1981. Characters, computers, and cladograms: a review of the Berkeley cladistics workshop. *Syst. Bot.* **6**: 359–372.
- CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia Univ. Press, New York.
- DAHLGREN, R. M. T., & H. T. CLIFFORD. 1982. The monocotyledons. A comparative study. Academic Press, New York.
- & F. N. RASMUSSEN. 1983. Monocotyledon evolution. Characters and phylogenetic estimation. In: M. K. HECHT, B. WALLACE, & G. T. PRANCE, eds., *Evolutionary biology*. Vol. **16**. Pp. 255–395. Plenum Press, New York.
- DANIELS, G. S. 1978. Lectotypification of *Heliconia platystachys* (Musaceae). *Kew Bull.* **32**: 681, 682.
- & F. G. STILES. 1979. The *Heliconia* taxa of Costa Rica. Keys and descriptions. *Brenesia* **15**(Supl.): 1–150.
- DODSON, C. H., & A. H. GENTRY. 1978. Heliconias (Musaceae) of the Río Palenque Science Center, Ecuador. *Selbyana* **2**: 291–299.
- ELDREDGE, N., & J. CRACRAFT. 1980. *Phylogenetic patterns and the evolutionary process*. Columbia University Press, New York.
- EMYGDIO, L. DE MELLO FILHO. 1975. O gênero *Heliconia* na flora fluminensis de Frei José Mariano da conceição Vellozo. *Revista Brasil. Biol.* **35**: 331–337.
- . 1976. *Heliconiae novae Brasiliensis*. III. *Bradea* **11**: 91–94.
- ENGLER, A. 1900. *Das Pflanzenreich*. IV. **45**. Musaceae (K. SCHUMANN). Wilhelm Engelmann, Leipzig.
- . 1902. *Das Pflanzenreich*. IV. **48**. Marantaceae (K. SCHUMANN). Wilhelm Engelmann, Leipzig.
- . 1904. *Das Pflanzenreich*. IV. **46**. Zingiberaceae (K. SCHUMANN). Wilhelm Engelmann, Leipzig.

- . 1912. Das Pflanzenreich. IV. 47. Cannaceae (FR. KRÄNZLIN). Wilhelm Engelmann, Leipzig.
- & K. PRANTL. 1889. Musaceae, Zingiberaceae, Cannaceae, Marantaceae. Die natürlichen Pflanzenfamilien, II. 6: 1–43. Wilhelm Engelmann, Leipzig.
- & ———. 1930. Musaceae, Cannaceae, Zingiberaceae, Marantaceae. Die natürlichen Pflanzenfamilien, II. 15a: 505–693. Wilhelm Engelmann, Leipzig.
- ERDTMAN, G. 1966. Pollen morphology and plant taxonomy. Almqvist & Wiksell, Stockholm. (Offset edition with addendum, Hafner, New York.)
- FARR, E. R., J. A. LEUSSINK, & F. A. STAFLEU. 1979. Index nominum genericorum. Vol. 1. Bohn, Scheltema & Holkema, Utrecht.
- FARRIS, J. S. 1970. Methods for computing Wagner trees. Syst. Zool. 19: 83–92.
- GATIN, M. C.-L. 1908. Recherches anatomiques sur l'embryon et la germination des Cannacées et des Musacées. Ann. Sci. Nat. Bot. 8: 113–146.
- GREEN, P. 1969. Notes on Melanesian plants. II. Old World *Heliconia* (Musaceae). Kew Bull. 23: 471–478.
- GRIGGS, R. F. 1903. On some species of *Heliconia*. Bull. Torrey Bot. Club 30: 641–664.
- . 1904. Two new species of American wild bananas with a revision of the generic name. *Ibid.* 31: 445–447.
- . 1915. Some new species and varieties of *Bihai*. *Ibid.* 42: 315–330.
- HENNIG, W. 1966. Phylogenetic systematics. (Translated by D. D. DAVIES & R. ZANGERL.) Univ. Illinois Press, Urbana.
- HUMPHREY, J. E. 1896. The development of the seed in the Scitamineae. Ann. Bot. 10: 1–40.
- HUTCHINSON, J. 1934. Families of flowering plants. ed. 1. Vol. 2. Monocotyledons. Clarendon Press, Oxford.
- . 1959. Families of flowering plants. ed. 2. Vol. 2. Monocotyledons. Clarendon Press, Oxford.
- KLUGE, A. G., & J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18: 1–32.
- KRESS, W. J. 1981a. New Central American taxa of *Heliconia* (Heliconiaceae). J. Arnold Arbor. 62: 243–260.
- . 1981b. Systematics and reproductive biology of Central American *Heliconia* (Heliconiaceae). Unpubl. Ph.D. dissertation, Duke University, Durham, North Carolina.
- . 1983a. Self-incompatibility in Central American *Heliconia*. Evolution 37: 735–744.
- . 1983b. Crossability barriers in Neotropical *Heliconia*. Ann. Bot. (London) 52: 131–147.
- . (in press). Pollination and reproductive biology of *Heliconia*. In: W. G. D'ARCY, ed., The natural history of Panama. Missouri Bot. Garden, St. Louis.
- & D. E. STONE. 1982. Nature of the sporoderm in monocotyledons, with special reference to the pollen grains of *Canna* and *Heliconia*. Grana 21: 129–148.
- & ———. 1983. Morphology and phylogenetic significance of exine-less pollen of *Heliconia* (Heliconiaceae). Syst. Bot. 8: 149–167.
- , ———, & S. C. SELLERS. 1978. Ultrastructure of exine-less pollen: *Heliconia* (Heliconiaceae). Amer. J. Bot. 65: 1064–1076.
- KUNTZE, O. 1891. Revisio generum plantarum. Pars I. Arthur Felix, Leipzig.
- LANE, I. E. 1955. Genera and generic relationships in Musaceae. Mitt. Bot. Staatssaml. München 13: 114–131.
- LINHART, Y. B. 1973. Ecological and behavioral determinants of pollen dispersal in hummingbird-pollinated *Heliconia*. Amer. Naturalist 107: 511–523.
- LINNAEUS, C. 1753. Species plantarum. Vol. 2. (1957 facsimile of ed. 1, Ray Society, London.)
- . 1771. Mantissa plantarum. (1961 facsimile reproduction, J. Cramer, Weinheim.)

- LUNDBERG, J. G. 1972. Wagner networks and ancestors. *Syst. Zool.* **21**: 398–413.
- MACBRIDE, F. 1936. Flora of Peru. Musaceae. *Field Mus. Nat. Hist., Bot. Ser.* **13**: 717–726.
- MAHANTY, H. K. 1970. A cytological study of the Zingiberales with special reference to their taxonomy. *Cytologia* **35**: 13–49.
- MAYR, E. 1957. Species concepts and definitions. *In*: E. MAYR, ed., *The species problem*. Amer. Assoc. Adv. Sci. Publ. **50**: 1–22.
- . 1969. *Principles of systematic zoology*. McGraw-Hill, New York.
- MILLER, P. 1754. *The gardeners dictionary*. ed. 4. Vol. 1. J. & F. Rivington, London.
- . 1768. *The gardeners dictionary*. ed. 8. Vol. 1. J. & F. Rivington, London.
- MIQUEL, F. 1859. *Heliconiopsis*. *Flora Indiae Batavae* **3**: 590. C. G. van der Post, Amsterdam.
- NAKAI, T. 1941. Notulae ad plantas Asiae Orientalis (XVI) [the Amomales or Zingiberales]. *J. Jap. Bot.* **17**: 189–203.
- PETERSEN, O. G. 1890. Musaceae. *In*: C. F. P. VON MARTIUS & A. W. EICHLER, eds., *Fl. Brasil.* **3**: 1–28.
- PLUMIER, P. C. 1703. *Nova plantarum Americanarum genera*. Joannem Bondot, Paris.
- SANTOS, E. 1978. Revisão das espécies do genero *Heliconia* L. (Musaceae s.l.) espontaneas na região Fluminense. *Rodriguésia* **30**: 99–221.
- SCHUMANN, K. 1900. Musaceae. *In*: A. ENGLER, ed., *Pflanzenr.* IV. **45**: 1–45. Wilhelm Engelmann, Leipzig.
- SIMPSON, G. G. 1961. *Principles of animal taxonomy*. Columbia Univ. Press, New York.
- SKUTCH, A. F. 1933. The aquatic flowers of a terrestrial plant, *Heliconia bihai* L. *Amer. J. Bot.* **20**: 535–544.
- SMITH, R. R. 1968. A taxonomic revision of the genus *Heliconia* in Middle America. Unpubl. Ph.D. dissertation, University of Florida, Gainesville.
- . 1975. Two new species of *Heliconia* (Musaceae) from the Canal Zone and Panama. *Phytologia* **30**: 65–70.
- . 1977. *Heliconia* in Nicaragua. *Ibid.* **36**: 251–261.
- . 1980. Musaceae. *In*: F. C. SEYMOUR, ed., *A checklist of the vascular plants of Nicaragua*. *Phytologia Mem.* **1**: 95, 96.
- STAFLEU, F. A., ed. 1978. *International code of botanical nomenclature*. Bohn, Scheltema & Holkema, Utrecht.
- STANDLEY, P. C. 1937. Flora of Costa Rica. Musaceae. *Field Mus. Nat. Hist., Bot. Ser.* **18**: 182–185.
- & J. A. STEYERMARK. 1952. Flora of Guatemala. Musaceae. *Fieldiana, Bot.* **24**: 178–186.
- STEBBINS, G. L. 1974. *Flowering plants—evolution above the species level*. Harvard Univ. Press, Belknap Press, Cambridge, Massachusetts.
- STEVENS, P. F. 1980. Evolutionary polarity of character states. *Ann. Rev. Ecol. Syst.* **11**: 333–358.
- STILES, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* **56**: 285–301.
- . 1978. Ecological and evolutionary implications of bird pollination. *Amer. Zool.* **18**: 715–727.
- . 1979. Notes on the natural history of *Heliconia* (Musaceae) in Costa Rica. *Brenesia* **15**(Supl.): 151–180.
- . 1980. Further data on the genus *Heliconia* (Musaceae) in northern Costa Rica. *Ibid.* **18**: 147–154.
- STONE, D. E., S. C. SELLERS, & W. J. KRESS. 1979. Ontogeny of exineless pollen in *Heliconia*, a banana relative. *Ann. Missouri Bot. Gard.* **66**: 701–730.
- , ———, & ———. 1981. Ontogenetic and evolutionary implications of a neo-

- tenous exine in *Tapeinochilos* (Zingiberales: Costaceae) pollen. Amer. J. Bot. **68**: 49–63.
- TAKHTAJAN, A. L. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. (Lancaster) **46**: 225–359.
- TOMLINSON, P. B. 1959. An anatomical approach to the classification of the Musaceae. J. Linn. Soc., Bot. **55**: 779–809.
- . 1962. Phylogeny of the Scitamineae—morphological and anatomical considerations. Evolution **16**: 192–213.
- WATROUS, L. E., & Q. D. WHEELER. 1981. The out-group comparison method of character analysis. Syst. Zool. **30**: 1–11.
- WILEY, E. O. 1978. The evolutionary species concept reconsidered. Syst. Zool. **28**: 88–92.
- . 1981. Phylogenetics—the theory and practice of phylogenetic systematics. J. Wiley & Sons, New York.
- WOODSON, R. E., JR., & R. W. SCHERY. 1945. Flora of Panama. Musaceae. Ann. Missouri Bot. Gard. **32**: 48–57.

DEPARTMENT OF BOTANY
DUKE UNIVERSITY
DURHAM, NORTH CAROLINA 27706

Present address:
THE MARIE SELBY BOTANICAL GARDENS
811 SOUTH PALM AVENUE
SARASOTA, FLORIDA 33577

EXPLANATION OF PLATES

PLATE I

Three species of the *trichocarpa* group. A, B, *Heliconia necrobracteata*: A, inflorescence, $\times 0.2$; B, flower, $\times 1$. C, D, *H. maculata*: C, inflorescence, $\times 0.14$; D, flower, $\times 0.8$. E, F, *H. talamancana*: E, inflorescence, $\times 0.1$; F, flower, $\times 0.8$.

PLATE II

Two species of the *trichocarpa* group. A, C, *Heliconia colgantea*: A, inflorescence, $\times 0.1$; C, flower, $\times 1$. B, D, *H. trichocarpa*: B, inflorescence, $\times 0.1$; D, flower, $\times 1$.

PLATE III

Three species of the *nutans* group. A, B, *Heliconia marginata*: A, inflorescence, $\times 0.25$; B, flower, $\times 0.75$. C, D, *H. secunda*: C, inflorescence, $\times 0.18$; D, flower, $\times 0.75$. E, F, *H. nutans*: E, inflorescence, $\times 0.25$; F, flower, $\times 1$.

PLATE IV

Two species of the *nutans* group. A, C, *Heliconia platystachys*: A, inflorescence, $\times 0.08$; C, flower, $\times 1.5$. B, D, *H. collinsiana* var. *collinsiana*: B, inflorescence, $\times 0.14$; D, flower, $\times 1$.

PLATE V

Species of the *curtispatha* group. A, C, *Heliconia curtispatha*: A, inflorescence, $\times 0.1$; C, flower, $\times 0.9$. B, D, *H. stilesii*: B, inflorescence, $\times 0.18$; D, flower, $\times 0.8$.

PLATE VI

Two species of the *pogonantha* group. A, C, *Heliconia sessilis*: A, inflorescence, $\times 0.13$; C, flower, $\times 1.5$. B, D, *H. mariae*: B, inflorescence, $\times 0.18$; D, flower, $\times 1.5$.

PLATE VII

Two species of the *pogonantha* group. A, C, *Heliconia pogonantha* var. *veraguasensis*: A, inflorescence, $\times 0.08$; C, flower, $\times 0.75$. B, D, *H. ramonensis* var. *lanuginosa*: B, inflorescence, $\times 0.1$; D, flower, $\times 1$.

PLATE VIII

Three species of the *pogonantha* group. A, D, *Heliconia danielsiana*: A, inflorescence, $\times 0.1$; D, flower, $\times 0.8$. B, E, *H. magnifica*: B, inflorescence, $\times 0.1$; E, flower, $\times 0.8$. C, F, *H. xanthovillosa*: C, inflorescence, $\times 0.1$; F, flower, $\times 0.75$.

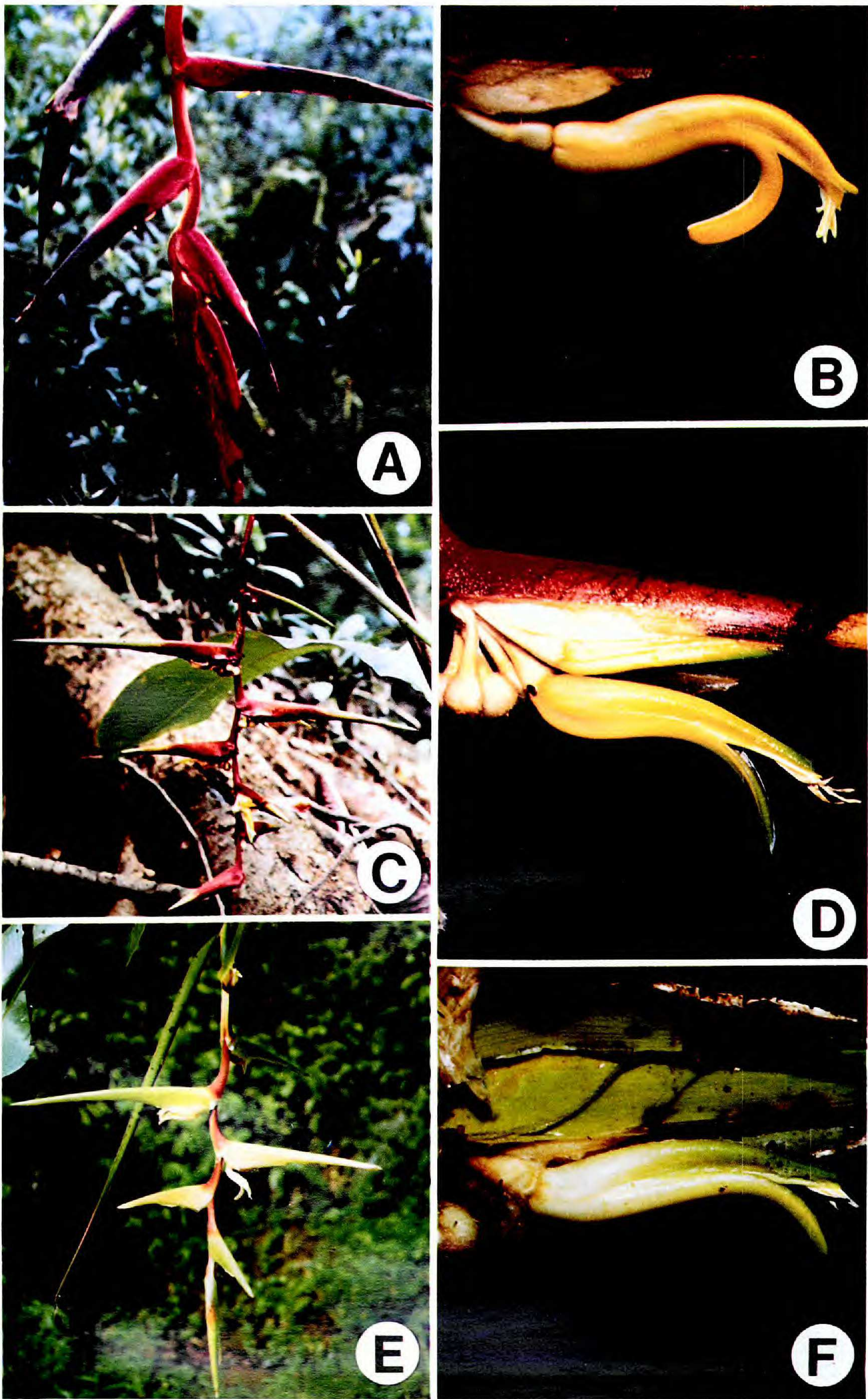


PLATE I

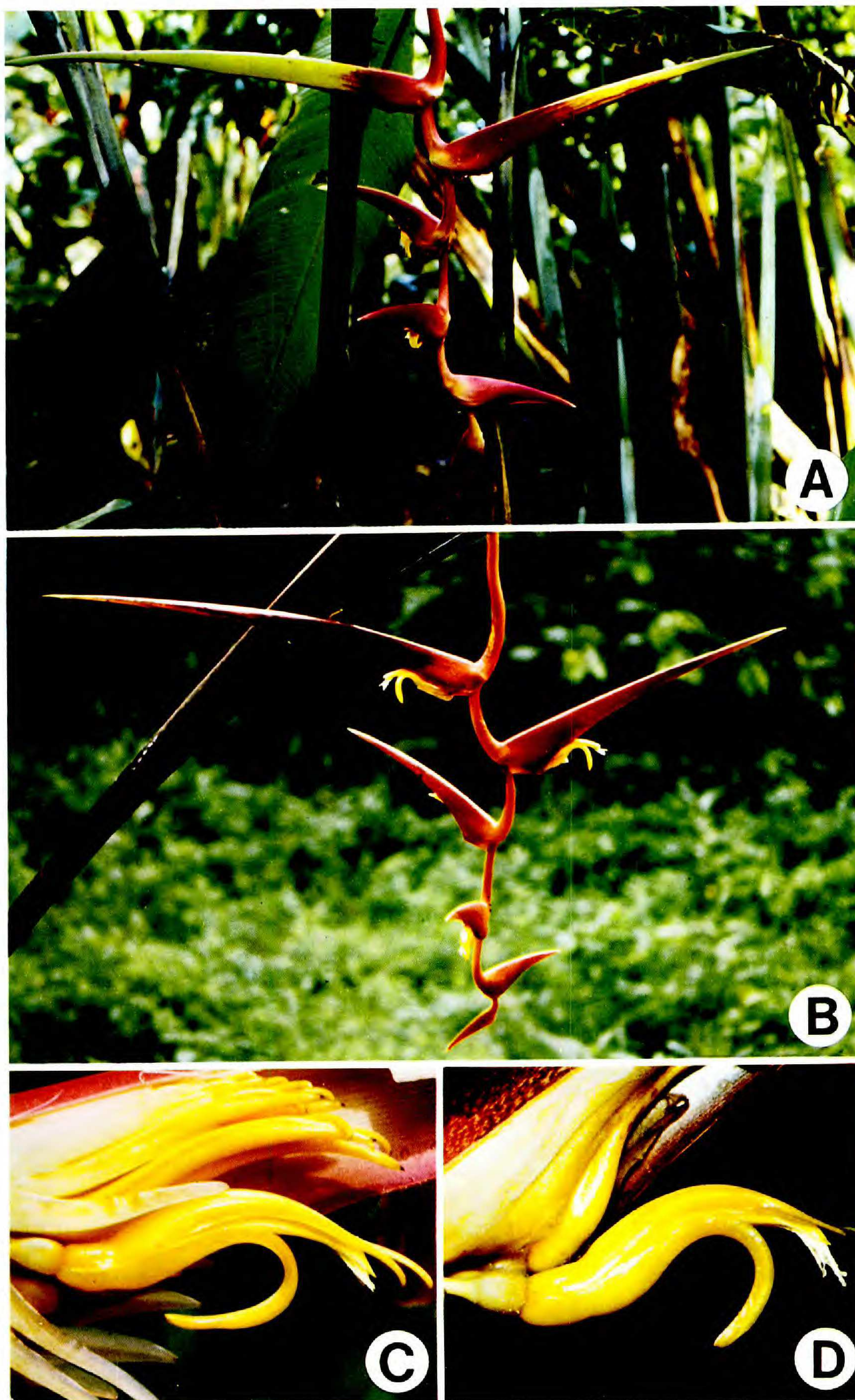


PLATE II

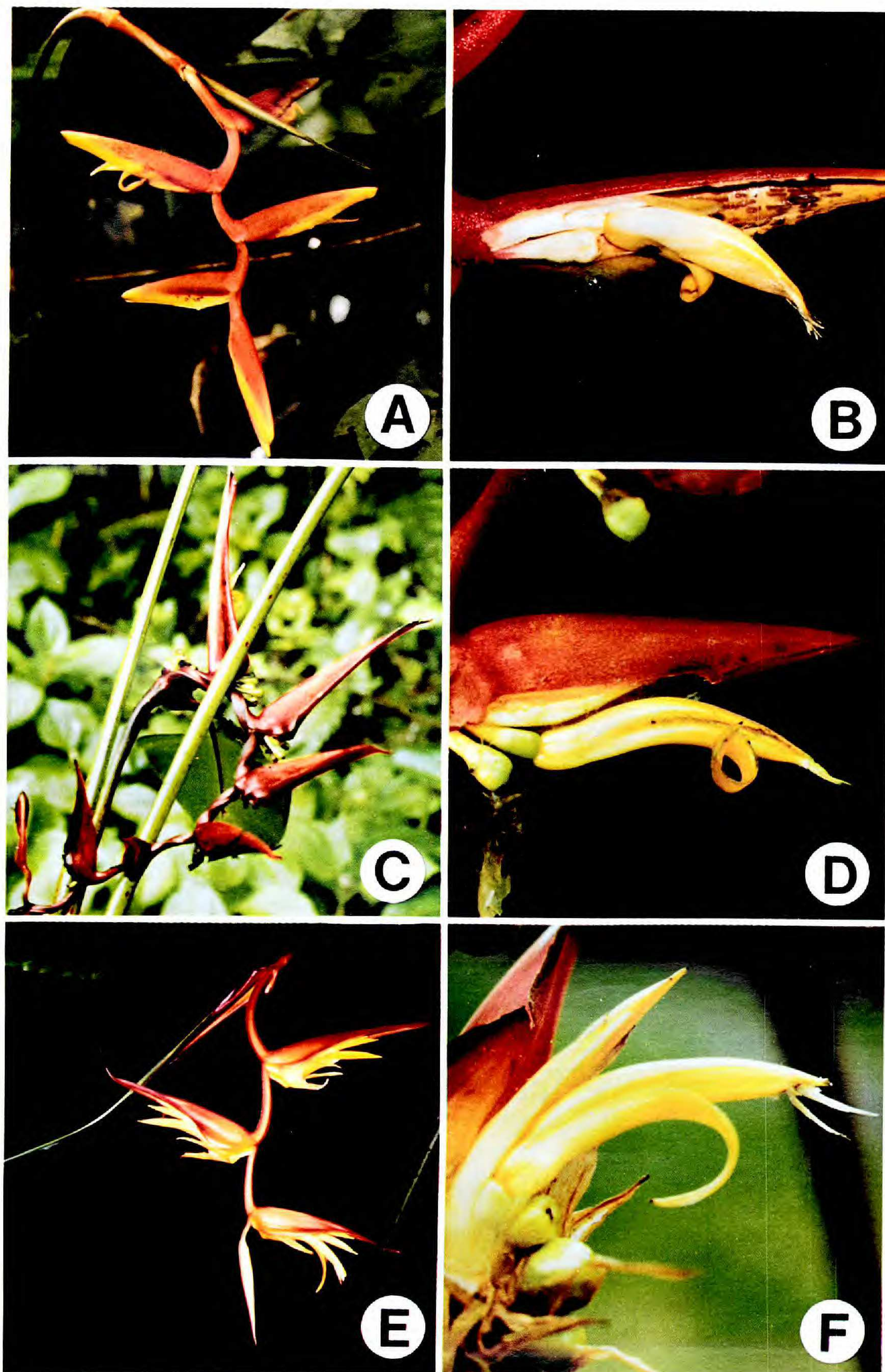


PLATE III

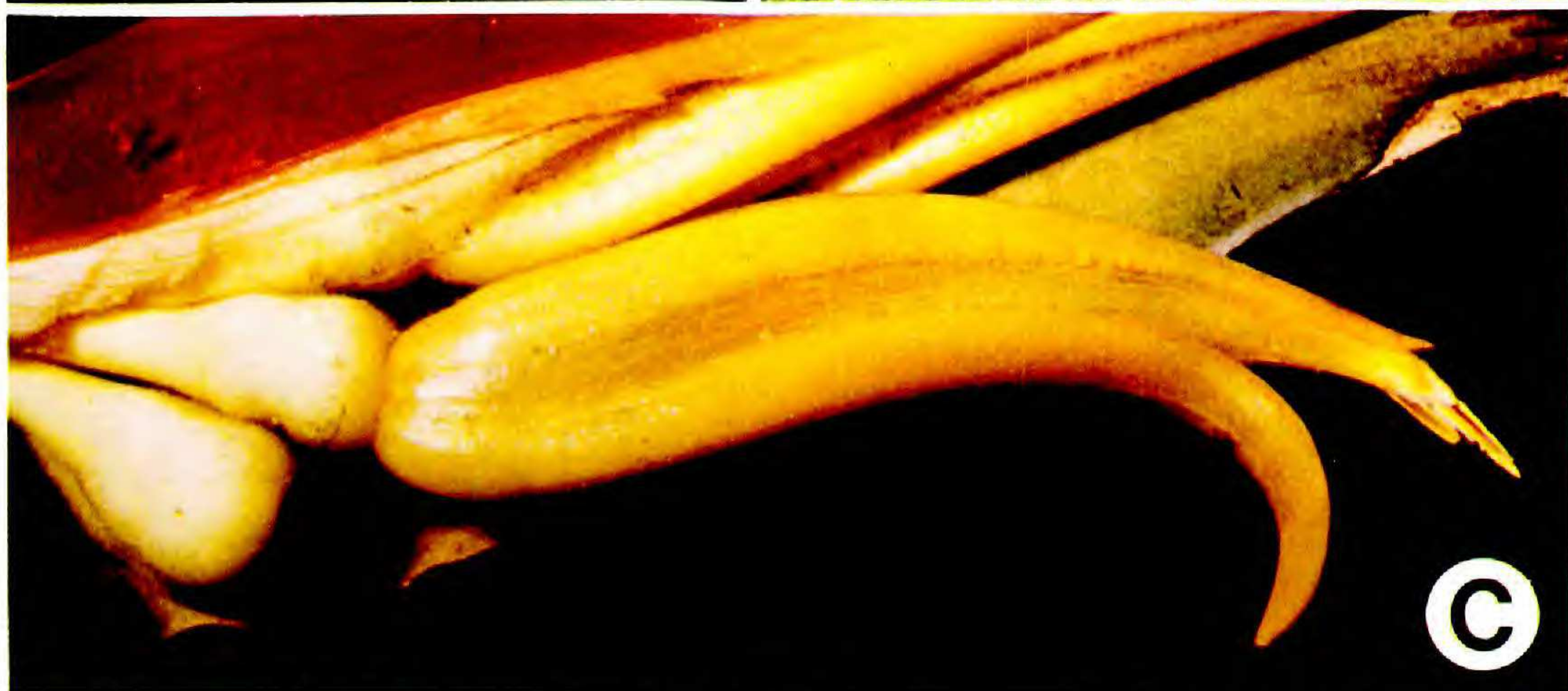


PLATE IV

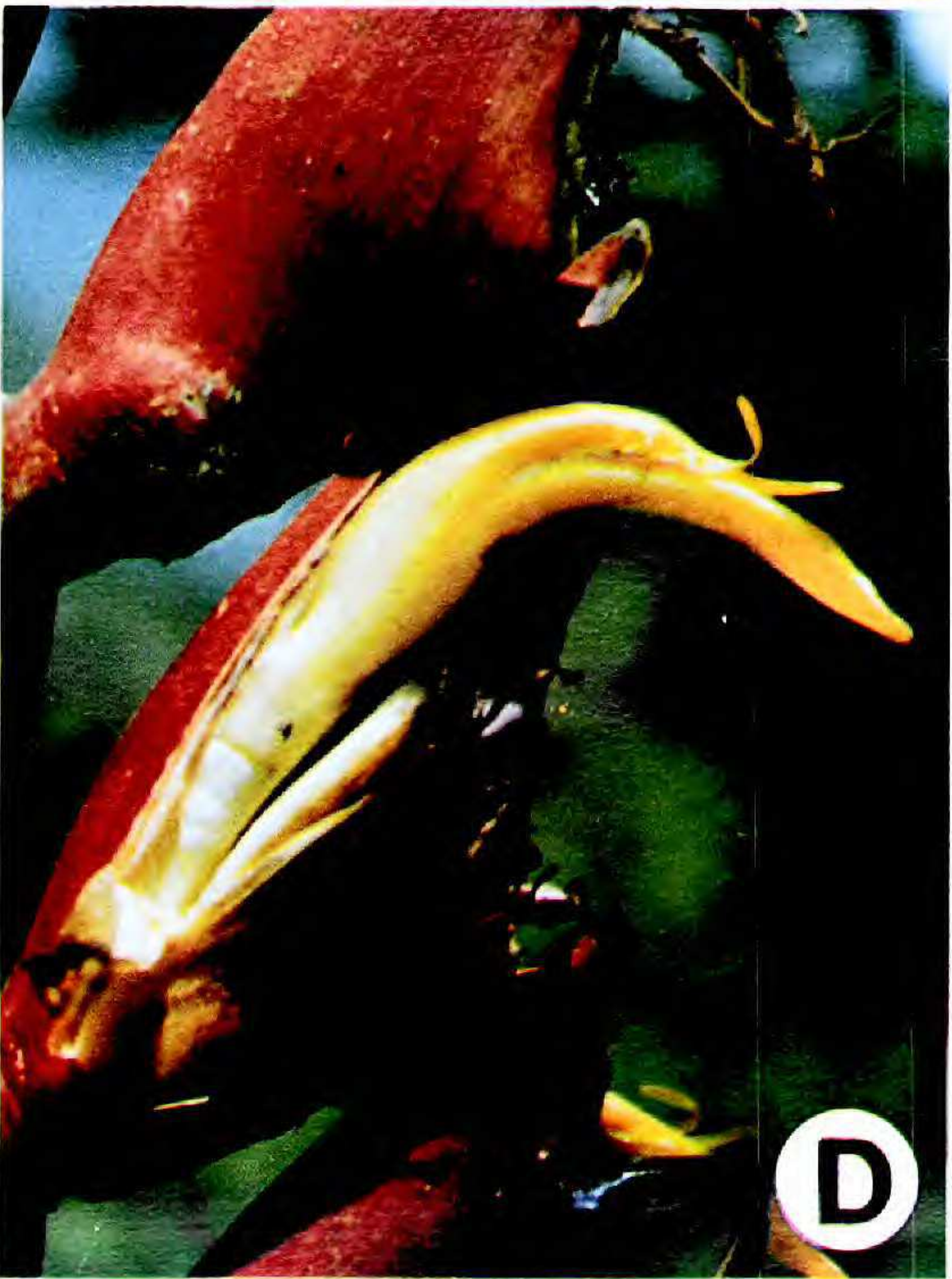


PLATE V



PLATE VI



PLATE VII

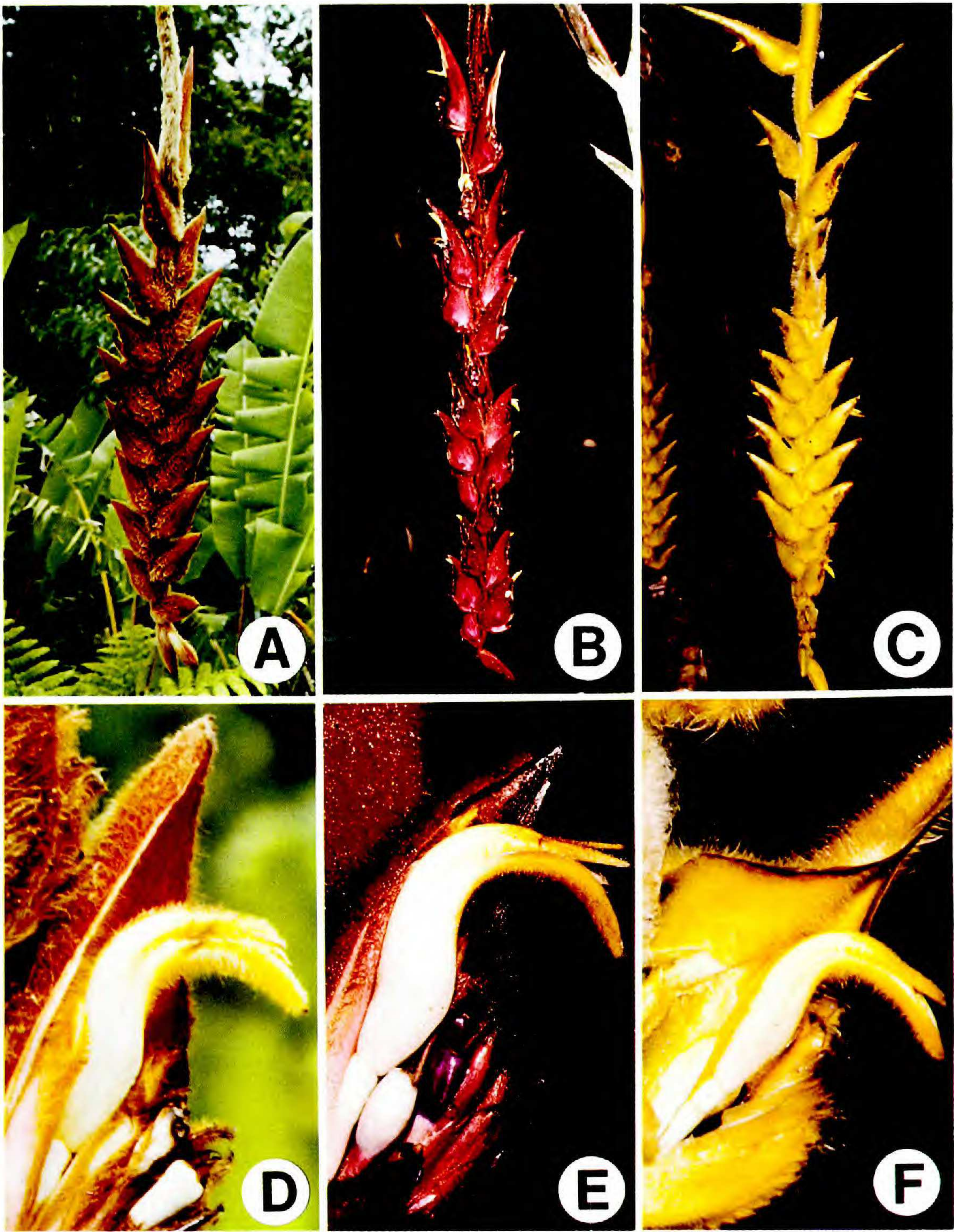


PLATE VIII